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RADIATION GENETICS

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I. INTRODUCTION

THE effectiveness of high-frequency radiation in the production of heritable changes in abundance, reported by Muller in his work with *Drosophila* and corroborated by the independent work of Stadler with plants, opens to the geneticists a method to speed the investigations of their problems. Some irradiation had been done earlier than the reports by Muller and Stadler; but it was not until after 1927 that an intensive use of radiation in genetics occurred. Many plants and animals have been subjected to irradiation, and in most of them genic and chromosomal changes have been induced. Irradiation not only supplies geneticists with a tool for the investigation of old problems, but also opens to them new problems and new methods of advance.

II. REGIONS OF THE SPECTRUM INVESTIGATED

Investigations have not been confined to natural (earth) radiation, x-rays and radium emanations, but have been carried into the low-frequency range.

Supersonic vibrations

Drosophila males were subjected to 285,000 vibrations for 25 seconds. In 26,135 possibilities appeared 57 abnormal individuals, including 5 with mottled eyes. Only the mottled eyes were hereditary. The results are inconclusive that the variants were caused by the treatment, but it is definitely shown that the supersonic vibrations used here do not produce effects comparable to those produced by x-rays and radium (110).

Electricity

Treatment of *Drosophila* males in a field between two concentric copper cylinders with a current of air passing through the space between the cylinders, 33,000 volts at 60 cycles, was given in dosages from 1 to 30 minutes. Treated individuals showed the effect; but no lethal mutations were induced, although some variants were observed (116).

Electrostatic

Drosophila males were subjected to 225,000 volts at a frequency of an oscillat-

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ing current of 1,225,000 cycles per second for one minute. Six hundred and ninety matings were made to observe for lethals, but no mutations were observed (116). After being subjected to an oscillating current of 6,000,000 cycles per second, wave length 200 meters, time 30 seconds, *Drosophila* males showed the effect of treatment. Only 35 per cent of the individuals were fertile. In 1607 cultures, no translocations or visible mutations were induced and the lethal-mutation rate was not significantly greater than that of the controls (241).

Electromagnetic

After exposure of pollen, a few recessive mutations were observed in maize. Ear shoots exposed between poles of a magnet 24 or 36 hours after pollination for 15 to 45 minutes produced endosperm mosaics two or three times as numerous as did controls. The frequency of mosaics increased with exposure increase, but not proportionally. Induced translocations also were indicated (253). Stadler (262) also reported that the method induces mutations in barley.

Ultra-violet

A quartz mercury arc with *Drosophila* under a quartz cover and cooled by iced air was used with treatment given to eggs, larvae, and adults. Earlier results by Altenburg (2) suggested that the method is not as effective as x-rays, but later results were found to be significantly effective. Thirty-four mutants were found in 11,502 treated to 3 in 11,162 control individuals (3, 4). Permanent and temporary modifications in *Chilodon* after treatment were observed by MacDougall (133, 134). Middleton induced a heritable change in the fission rate of *Paramecium*. Stubbe reported (274) that about 85.7 per cent of treated *Antirrhinum* produced altered F_1 as against 2.07 per cent in controls. This method has also been used by Goodspeed.

Grenz rays

Ultra soft x-rays generated at 7 KVP (262) or 5–10 (274) are sufficient to induce mutations. The induced mutation rate was increased 300 per cent over controls in *Antirrhinum* (277). Goodspeed has also found the method effective. The Beta rays of radiothorium and Cathode rays are also effective in the induction of mutations (262, 135).

III. RESULTS OBTAINED WITH X-RAYS AND RADIUM

Chromatin distribution

The percentage of primary non-disjunction in *Drosophila melanogaster* is significantly increased by x-radiation of the female (5, 6, 137, 138, 139, 143), and by radium treatment (164). The exceptions appear during the decreased fertility of females (143) and from eggs deposited the first six days after treatment (137, 234).

Aging eggs in the female before treatment increases the percentage of non-disjunction, although aging alone will not cause an increase. The frequency increase is gradual up to the eighth day, after which a decided decrease occurs, probably due to the fact that virgin females deposit their mature eggs in the eighth day (219, 234).

Exceptional males occur more frequently than exceptional females (139). Anderson (10) reported 631 exceptional males to 113 exceptional females among 57,877 offspring from the x-rayed *Drosophila* mothers. Patterson and coworkers (234) observed 330 exceptional males to 46 females in 90,000 offspring in the treated series and 55 non-disjunctional males to 8 females in a like number of controls. With *Dro-*

sophila virilis, Demerec and Farrow (44) reported a greater variation between the male and female ratio. In the treated series, 338 exceptional males to 17 females appeared in 65,809; and in the controls 23 to 2, in 37,188 offspring. Only two of the tested primary exceptions gave a high frequency of secondary exceptions and of crossing over (6, 9), and one of these has been found to involve a translocation (51). Age as shown by two successive broods does not alter the percentages of secondary exceptions in these lines (8).

Crossing over in the eosin-miniature region of the X-chromosome of *Drosophila* decreases in frequency as a result of x-ray treatment (140) and increases in the regions on both sides of the spindle fiber attachment of II (148, 149). Radium influence is similar to that of x-rays (235). The effect on crossing over is not inherited (150), and is due to the direct action of x-rays on the germ cells; no increase occurs unless at least the posterior half of the body is treated (146). A regional differential susceptibility to x-rays (II and III) was observed by Muller (165) who also found that the X does not differ from II or III if corresponding regions with relation to the spindle fiber are compared (166). Stadler (255) detected no influence of x-radiation on crossing over in maize. Combinations of temperature and irradiation (temperature before and after treatment) cause variations in the frequency of crossing over (126). Mavor and Svenson (151) have also made a comparative study of the influence of temperature and irradiation on crossing over.

Lethal and visible mutations

Antirrhinum after radium treatment developed abnormalities that were inherited by vegetative reproduction (265, 266); tissues were modified (268); and some variants apparently were results of gene mutations (269). X-radiation altered 87 per cent of the treated parents to 2 per cent in controls (274).

Bacteria seem to be more stable. Irradiation caused no variation in *B. coli* and only a tendency towards lack of ability to produce red pigment in *Erythrobacillus prodigiosus* (37). Other fungi have been investigated by Holweck and Lacassagne (*Saccharomyces*), by Nadson and Phillipov who have been able to select new and stable races, and by Svenson (*Saprolegnia*) who found negative results.

Barley mutants were observed in tillers (53 in 2800 treated head progenies, none in 1500 controls) after x-ray and radium treatment (254, 258). The tested mutants bred true, but among them no clear case of dominance was observed (258).

Chickens that developed from fertile eggs subjected to x-rays (120) showed the influence of the irradiation.

After x-ray treatment of cotton seeds, dwarfed plants and in other cases cotyledon and plant mutations appeared, some of them heritable (117, 118, 119). Induced variations of seeds and lint were also observed by McKay and Goodspeed.

Datura subjected to radium treatment had induced both gene and chromosomal mutations (11, 23, 64). Treatment of pollen induced lethal gene-mutations that caused half the pollen to be eliminated in male gametophytes; however, the genes may be inherited through the female gametophyte (28, 30, 31, 33) but pollen abortion also may be due to induced chromosomal abnormalities (34).

Drosophila funebris males after x-radiation gave a higher frequency of sex-linked lethal and visible mutations, the latter for the most part of wings and bristles (280, 281). *Drosophila obscura* responds to irradiation (162, 242), and *Drosophila melanogaster* has been used repeatedly in irradiation experiments. Muller reported

an increase in the mutation frequency of 15,000 per cent when sperm were subjected to x-rays; five lethal mutations were found in 6016 control chromosomes; 59 in 714 chromosomes given a T_2 dosage, and 142 in 1177 T_4 chromosomes (168, similar ratio 170). Induced changes involve all gradations of lethality and visibles; those resembling known mutants, at new loci, new genotypes but old phenotypes, and many extreme allelomorphs (167, 168, 174). Weinstein (295,) Hanson (93), and Demerec and Anderson corroborated the effectiveness of x-rays in producing changes. Visible mutations, new and old types, were increased 1200–1600 per cent by Grüneberg (86), and have been reported by Hanson (94), Mavor (147), Serebrovsky and Dubinin (244) and other investigators. After radium treatment, 204 induced mutations were observed in 14,480 offspring by Hanson and Winkleman. Mutations also are induced in somatic tissue by x-rays (78, 217, 283). Patterson (217) observed 42 variant areas of the eye among 1473 treated to none in 1789 control individuals (also see 218, 219). Dominant eye colors in *Drosophila melanogaster* appeared for the first time in irradiation experiments. Weinstein (295, 296) observed the first dominant eye-color (typical, eversporting type). Oliver (198, see also 174) found a solid color, non-eversporting, but connected with a chromosomal alteration. Van Atta (293, 294) detected a dominant due to a definite gene (no connection with a chromosome aberration).

Grape fruit seeds exposed to x-rays developed into plants, some of which showed seedling variations (161).

Habrobracon mutants were found by Whiting (301, 303, 304, 305) and by Dunning as a result of x-ray treatment. Induced non-inherited freaks and mutations occurred after larvae treatment (297, 299) and after adult male (36) and female (25) treatment.

Mice subjected to x-ray treatment produced descendants among which abnormalities occurred (130, 131), and the abnormal eye individuals show no variation in chromosome number or morphology (210). Variant types observed by Dobrovolskaia-Zavadskaia were interpreted as not induced by the treatment. Snyder (251) found no induced visible modifications in rats.

Nicotiana has been used extensively in irradiation experiments, and as a result of x-ray treatment developed vegetative and floral changes and gene mutations (68, 70, 73, 74, 76, 77).

Oenothera buds after being subjected to radium treatments developed atypical forms (26).

Sorghum responded to x-ray treatment, and four induced recessive mutations bred true (Horlacher, Karper and Quinby, reported for 201).

Tomato leaf and floral abnormalities were observed by Johnson. McArthur and Lindstrom exhibited recessive plant characters and also seedling characters that were induced by x-ray, radium and cathode treatments (135).

Triticum variant types were observed by Delaunay (41, 42), Stadler (see VI), and Sapehin.

Other organisms are given under subsequent headings.

Chromosomal mutations

Translocations are induced with x-ray treatment of *Drosophila melanogaster* sperm (167, 168, 169, 295), with a frequency equal to that of gene mutations (170, 178, 179, 199, 200). Oliver reported 21 lethals, 16 CA (most being inversions), and 17 translocations occurring in 105 individuals from t_{16} treated parents, and 18 lethals, 13 CA, and 10 translocations all involving

the X in 411 offspring from t_4 treated parents (200).

Most induced translocations are probably of a simple type (214). This type has been observed by Dobzhansky and others working with *Drosophila*, by Nabours and by Robertson with *Apotettix*, and by Blakeslee (23) with *Datura*. Of the thirty translocations studied in maize, none were simple; all were reciprocal or involved a deficiency at the point of translocation (152). Mutual or reciprocal translocations have also been observed in *Drosophila* (24, 51, 54, 57, 173, 278, 294), and abnormal configurations were explained as due to reciprocal translocations in *Datura* (20, 23), and in *Circotettix verruculatus* (109). The more complex translocations may involve a deletion of one chromosome (II to Y, 50, 51, 53, 236; X to IV, 185; X to III, III to X, 198, 200), or multiple fragmentation, probably inversions in the donor or recipient chromosome (51, 198, 200, 294).

Homozygous translocations observed in *Drosophila* usually prove to be lethal or sterile, or exhibit abnormalities (52 and earlier, 174, 178, 179), although some do not (47). Bergner and coworkers (21) also reported a homozygous translocation in *Datura* that breeds true. Individuals heterozygous for a translocation usually are normal in appearance, but in some cases visible effects accompany the fragmentation (174). Dobzhansky (54) and Van Atta (294) reported visible changes that are inseparable from a point of breakage.

Chromosomes may fragment or have a fragment attached to any point (48, 50, 170, 178, 183, 189, 295), and not always at constrictions (49, 214), although chromosomes may give way more readily at constrictions (128). The displaced fragment is usually attached to the end of the recipient chromosome (49, 51, 232), but the attachment may be along the side (57, 278) or the piece may be inserted (198, 200, III into X near ec). Any or all chromosomes may be involved in a translocation, with little or no preference except as a function of the length of the chromosomes (170, 178, 179). Most observed translocations are interchromosomal, but intra-chromosomal types may occur. Of the latter type, a fragment of X was deleted and attached to the right end of X (59, 244).

Inversions, deletions, and deficiencies (not necessarily translocations) have been observed in *Datura* (20), maize (67, 258, 261), *Secale* (128, 129), and *Drosophila* (183, 214, 244 and others), including inversions that cause a V shaped chromosome to have a terminal fiber attachment (202, 294).

Chromosomal irregularities were induced in *Datura* with a frequency of 10 per cent (20), and some of the new types cause aborted pollen (34). Lost satellites and fragmentations have been observed in *Crepis* (128, 189) and *Vicia* (128). Frequent rearrangements and losses were reported in maize (261). Variations in number and shape of chromosomes occurred in *Triticum* (41). Chromosomal irregularities were induced in *Nicotiana* (77), with fragmentation, non-disjunction, and duplication of fragments (68, 70, 75). Variations in the number of chromosomes as a result of treatment occurred in *Datura* (64), *Nicotiana* (68, 71, 73), and tulip (157, 158); but in maize no evidence of tetraploidy or duplication of whole chromosomes as a result of irradiation was observed (261).

Mosaic regions

If *Drosophila* eggs or larvae are treated with x-ray, variant colored areas appear in the eye. With a treated homozygous red female, no white areas were observed

in 217 individuals; with a female heterozygous white, 34 areas in 666; males not white, 8 areas in 807; and in the control males and females, none (217). Similar but larger ratios were observed by Patterson (218) and by Timofeeff-Ressovsky (283, 284). The latter also reported changes of eosin to white (2 in 1407), of eosin to red (1 in 1407), of white to red (1 in 2986), and of white to reddish allelomorph (1 in 2986). Patterson (218) also found mosaic areas for other traits, many of which have been exhibited (230). The greater frequency observed in females is explained as due to breakage of the X (217, 218, 219). The use of special stocks determined that in many or most cases the areas are due to fragmentations, and not to the elimination of the whole X (220). Gowen (78) also found the action in producing mosaic regions to be local as to III, the affected areas involving but one of the colors (st, ca) investigated. Mosaicism in *Habrobracon* was reported as a result of binuclearity (85, 300).

Germ cells of *Drosophila* treated with x-rays may develop mosaic individuals for parts of the body due to the loss of IV (49), or for mottled eyes involving the locus of white on X, or eversporting variegated eyes (see VII). Habrobracon after x-ray treatment had variant regions of eyes and wings (5 in 1721 treated, 6 in 8258 controls, reported in 297) but mosaics occur only in heterozygous females as a result of binuclearity (299).

In maize, treated embryos develop into chimeras; but if treatment is given on the first and second day after pollination the whole plant shows an absence of dominants. The areas are also observed if pollen is treated (258). Mosaic endosperms occur (255). The size of the variant area depends upon the time after fertilization that treatment is given (258). In a 20-fold increase as a result of irradiation, the mutated areas seemed to be due to a lack of a piece or all of a chromosome, as shown by the loss of dominant markers (255, 258, 261). Cotton was reported with splotched areas of virescent yellow and of green-white due to cytoplasmic disturbance or to abnormal chromosome behavior, and angular areas that were probably nuclear changes (117, 119). Heterozygous barred and also black-white chickens developed mosaic regions (15 areas in treated, to 4 in an equal number of controls, reported in 120). In mice, white areas replaced color (90), and such areas may be used as an index of sterility (125). Mosaic areas have occurred in *Nicotiana* as a result of treating germinated seeds and seedlings (68).

Sex mosaics

All of 23 sex mosaics found in *Habrobracon* by Dunning were sterile. In *Drosophila*, Mavor (144) reported 4 sex mosaics in 68,186 treated, and none in 65,128 control individuals. Of the 4, the treated X had been eliminated twice and the untreated X twice. Patterson determined that the sex mosaics were caused by elimination of the treated X in 32, and of the untreated X in 17 cases. Of the latter, 15 came from treated eggs and 2 from treated sperm. From these results Patterson (221, 223) concluded that if the sperm is treated, the treated X is more apt to be eliminated; if the egg is treated, either X with an equal frequency. If eggs are treated, generally the whole chromosome is eliminated and the mosaic is of the half-and-half type. This type alone is increased over that found in controls by irradiating the sperm cells (231).

Fertility and viability

Radium treatment of *Antirrhinum* may leave only females fertile, or neither sex fertile (267, 269). *Habrobracon* as a result

of treatment has a less number of females (60, 302, 25). In *Drosophila*, the decrease in fertility of treated males is interpreted by Muller as due in part to dominant lethals (167, 168), and Stancati using *Habrobracon* determined that the absence of biparentals is due to zygotic dominant lethals and not to an absence of viable sperm. Treatment of *Drosophila* females causes a decrease in fertility; but a partial recovery occurs, and the new eggs show a high proportion of mutant genes (167, 168). The effects of x-rays and age on fertility have been found by Patterson and coworkers (234) to be manifested chiefly on the fully formed eggs, no effect being apparent on immature eggs.

Snyder (250, 251) and Snell (248, 249) found that x-radiation produced infertility in rats and mice. The latter reported that the litters sired during the early fertility period were reduced in number, not as a result of a lack of motile sperm, but due to genetic changes lethal to embryos. Strandskov obtained similar results and conclusions with guinea pigs.

With treated dry or soaked seeds of *Nicotiana*, the initial rate of germination is retarded, but only temporarily (68), and treament does not lower the percentage of germination of good dry seeds of cotton (117, 119).

The effect of irradiation upon fertility and viability may also be observed among the offspring of treated individuals. In *Drosophila* the decrease is explained by Muller as due in part to dominant sterility genes (167, 168). The condition in maize is generally due to deficiencies and translocations rather than to gene mutations (258, 261).

IV. RESULTS WITH VARIATIONS IN TREATMENT

Variation in the duration of x-ray treatment of *Drosophila* males was found to produce a like variation in the mutation rate, although with the two dosages used the small numbers did not show the results proportional to dosage (93, 167, 168, 295). With a series of 5 regular steps, each dosage increase showed a significant increase in the induced F_3 lethal mutations (197, 200). Similarly an increase was observed with three dosages by Serebrovsky and Dubinin, by Efroimson for each series (hard rays, soft rays, and with Coolidge tube), and by Dunning with dosages between 1200–8000 R in an investigation of *Habrobracon* somatic abnormalities. The number of mutated somatic areas in *Drosophila* increases with a like variation in dosage, but size of the areas depends upon the age of the treated individuals (217, 218, 219).

Stadler (254, 256, 258) observed an increased frequency of mutations in barley with an increased x-ray intensity. Similar results were observed, but no actual measurements made, with cotton (117). Stubbe (277) reported that an increase in r-units (doubled each time) causes an increase in the percentage of gene mutations in *Antirrhinum*, but that the variations fluctuate irregularly.

Radium behaved similarly in that an increase in dosage applied to pollen caused a significant decrease in the rate of *Datura* pollen-tube growth (29). It has also been reported with *Drosophila* that as radium rays were screened with increasing thicknesses of lead, the percentage of F_2 lethals induced in males decreased consistently (95, 97).

An increase in voltage in x-ray treatment of *Drosophila* males (40 to 100 KV) caused an increase of F_2 lethals; doubling the voltage quadrupled the number of lethals (105, 107). The mutation rate in barley also increased with voltage increase (254).

Crossing over irregularities and translocations increased with the duration of

treatment to which *Drosophila* males were subjected (295). With two doses (one double the other) the frequency of translocations involving the X and crossing over irregularities of X for the higher dose occurred with a frequency twice that for the lower dose (199, 200). Treatment of young ears of maize with seven graded doses caused a graded increase in the number of deficiencies as observed in mosaic endosperm (67, 261).

Non-disjunction frequency in *Drosophila virilis* after x-ray treatment of the female increased rapidly and significantly only up to 1200 r-units, after which the increase was not so rapid (45).

That fertility progressively decreases with dosage increase has been observed in the number of offspring from treated *Drosophila* males and females (167, 295), and in a comparison of the mortality of eggs and larvae, and pupae (93). Snell found a similar decrease with mice. With eight graded steps for treated *Drosophila* females, fertility did not decrease rapidly until high dosages were used (45). A similar condition was observed by Oliver when males were treated in five graded steps (reported for 201). An increase in x-ray dosage causes a decrease in fertility of *Habrobracon*, whether males or females are treated (25, 60, 299, 302), the average number of progeny decreasing with increase in dosage. Three extremes of dosage were found by McCrady to produce three degrees of sterility in *Habrobracon* and three variations that may be observed cytologically. In *Datura* a marked difference in seed output per capsule and of plants obtained was observed with dosage steps of 0.16 millicurie hours (29).

Equivalent dosages (intensity) differently applied do not vary the results. Discontinuous treatments with measured intensities were used on barley, and an increase in the mutation rate was observed with added dosages (254). Serebrovsky and Dubinin found an increase in the mutation rate in *Drosophila* whether dosage was intermittent or continuous. In a test by Patterson (224) of continuous and spaced treatments with the total duration equal, no significant variation in the results occurred. Different x-ray voltages in equivalent treatments of barley seeds (KV from 40–116) induced mutations with an equal frequency (258). High intensity of radium treatments for brief, or low for long periods gave equivalent results with *Drosophila* (102, 103). In a comparison of x-ray and radium effectiveness based upon a study of the seed yield per capsule for *Datura*, Buchholz and Blakeslee (32) found the relative effectiveness of the two treatments to be comparable. Packard (206) has found a similar effectiveness for the two methods in an investigation of their biological effect.

Variations in conditions during treatment

Barley seeds soaked 7 hours in M/5 solutions and x-rayed 15 hours later were found to have a higher mutation rate as a result of the chemical impregnations (254). *Drosophila* males subjected to sulphuric ether during radium treatment gave an increased sterility and lethal mutation rate (101) as a result of the anaesthetic.

Results obtained when *Drosophila* males were given the same dosage (2300 r) but treated at 34°C., and at 8°C., indicate that temperature will not alter the effectiveness of irradiation (173). Stadler (256, 258) also found no variation in the mutation rate of dormant or germinating barley seeds irradiated at various temperatures (10–50°C.).

The relation between other physiological conditions and the mutation rate has been investigated in plants and animals. Mutations may be induced in dormant seeds, but at a lower rate than for

similarly treated germinating seeds. At high dosage, however, the rate for dormant seeds is as high as for germinating seeds at their limiting dosages (256, 258). The average yield of mutations per Roentgen unit in germinating seeds is about eight times that in dormant seeds (256, 262). This difference is not a question of water content. The rate for seeds soaked before treatment, but not germinating, is no higher than for dormant seeds (258). Chromatin in any metabolic condition of the cell, from dry seeds to mature sex cells, can by appropriate treatment with x-ray or radium be quantitatively or qualitatively altered, but dry or soaked seeds are more resistant in *Nicotiana* (68), cotton (117), barley (256, 262), and *Antirrhinum* (275). Muller (173) postulated from small numbers that the metabolic rate in *Drosophila* females (fed as against starved; impregnated against virgin) probably does not alter mutability significantly; but Hanson and Heys (101, 104) observed reduced sterility and mutability as a result of starvation before treatment.

Variations in conditions before and after treatment

If seeds are steeped for 14 hours, tolerance decreases to half that of dormant seeds. The first half hour of aeration again decreases tolerance by half; but the decrease is less marked during the next 4½ hours. Mutability increases slightly during the first two periods and then increases rapidly (262).

Germinating seeds subjected to various temperatures (7 to 37° for 24 hours following treatment) and dormant seeds (−80 to 38° for 24 hours after, and 5 to 38° for weeks after) have their mutation rate unaffected (262); however, *Habrobracon* males are more fertile if kept at low temperature for 14 days after treatment (302).

Aging of *Drosophila* sperm before treatment will not alter the induced mutation frequency (167, 288), nor will the rate of lethal mutations be altered if treated males are held as long as 16 days before mating (108, 98). In successive broods every 7 days after radium and x-ray treatment no change in the mutation rate occurred until the fourteenth day, after which there was a sudden drop (98). No significant change in the rate of sex-linked lethals occurred for 12 days in successive matings of males to virgin females every 4 days (108) and broods every 5 (288) or 6 days (61). Schapiro found that the percentage of translocations (II, III, IV) in successive matings to virgin females approximately every 6 days decreased rapidly after 16 days. On the other hand, Sidoroff observed about as many lethals in II during the second as during the first 14 days. Mutations occur in dormant seeds whether or not they are planted immediately after treatment, but the heavily treated seeds decrease in viability during storage (256, 258). Cotton seeds that had been stored for two years before treatment seemed to be more susceptible to x-radiation (117). Aging *Drosophila* females before treatment does make them more susceptible to irradiation in the induction of primary non-disjunction and in the breakage of the X-chromosome (219, 234).

V. SELECTIVE ACTIONS OF X-RAYS AND RADIUM

Sex-ratio

Irradiation of *Drosophila melanogaster* males causes a deviation in the sex-ratio in favor of more sons (16, 17, 61, 93, 168). This is explained as due for the most part to dominant lethals induced in X, the Y being inactive (61, 168). Barth (16, 17) found that if the males are mated to attached-X females, less sons than

daughters appear, in either case a differential susceptibility of X and Y sperm, resulting in a deficit of X sperm. With *Drosophila obscura*, a low ratio of female to male was reported by Morgan, Bridges, and Schultz (162), due possibly to many types of chromosomal aberrations (242). Treatment of *Habrobracon* females reduces the ratio of female offspring, probably due to injury to the sperm in the seminal receptacles (25, 302), or to induced dominant lethals (85).

On the other hand irradiation of *Drosophila* females causes no marked difference in the sex-ratio, and does not affect the potentiality of eggs to produce male or female (143). Neither is the sex-ratio altered by treatment of eggs and larvae (218); consequently, the mortality of larvae is considered by Muller (173) to be chiefly non-genetic.

Stage of maturity of sex cells

A differential effect upon early and later germ-cell stages is observed in treated *Drosophila*, with a less effect upon early male sex cells. This conclusion is based upon the observed decrease in the percentage of mutations that occurs twelve to fourteen days after treatment (see IV). The observed differential effect is explained as due to the fact that chromatin in mature male germ cells is more easily affected, or that germinal selections or selective multiplication occur against the affected immature cells (173, comparison of mature sperm as against larvae; and 108, 246, 288, differences in mutation rate over a length of time). Patterson (231) found evidence for a selective effect in the decided drop in fertility that occurred on the fourth day after irradiation. Strandskov suggests that lethals may be more readily produced in mature guinea pig sperm, but spermatogonia may also be affected. The susceptibility of immature cells is supported by the fact that reverse mutations of forked to not-forked occurred as frequently from treated *Drosophila* larvae as from treated sperm (232). In fact, mutations may be induced in all portions of the genital system of either sex (167, 168, 170). This is also suggested by the appearance of similar mutants in the same culture (217, 232).

In *Nicotiana*, the indications are that the stage of maturity of the sex-cells has little relation to the effectiveness of x-radiation (68); but in *Habrobracon*, the less mature eggs are sterilized more readily (302). A difference in the response of Cladoceran eggs in the brood pouch and the immature stages has also been referred to (194).

Sex

Mutations are induced in *Drosophila melanogaster* whether sperm or eggs are treated (167, 168, 170), but gene and chromosome irregularities occur more frequently in sperm than in oocytes for a given dose; and the ratio of chromsome to gene variants is greater in males than in females (173). Similarly in *Drosophila obscura* the effect of treatment is more noticeable on the males (162, 242). Somatic mutations occur more frequently in *Drosophila* females than in males (see III). A comparison of the response at the same stages in the life cycle indicated to Moore (160) that fertility is decreased more by treatment of males than of females. In *Antirrhinum* the gene mutation rate is higher in males than in females; but the rate of variation is higher in females (274, 277). *Habrobracon* male larvae are more susceptible than female larvae (299).

Other conditions

The mortality of treated eggs and larvae of *Drosophila* is high but older larvae are more resistant to irradiation (145, 218),

and the resistance increases after 30 hours of pupation to equal that of the adult (145). Woskressensky also found the adult flies to be more resistant, as did Hey with the bean weevil. A possible susceptibility of chromatin during a peculiar physio-chemical condition is seen in the multiple mutations per treated cell, and in the fact that treated adult males gave 111 abnormal F_1 males among 2964, to 20 among 2651 treated larvae 3–4 days old (173).

VI. GENETIC PRINCIPLES DETERMINED

Relation of dosage to genetic effects

The frequency of induced mutations is directly proportional to the intensity of treatment. In the plant group it has been found that with dormant or germinating seeds of barley, the mutation rate is proportional to x-ray intensity (256, 258), to the amount of radium treatment, or of any given radiation (262). Proportionality does not apply to the frequency of induced defective maize seeds, for the rate rises sharply with higher dosages (261). Variations in *Antirrhinum* are not induced proportionally to x-ray intensity (274, 277), although gene mutations are (277). Leaf variegations in cotton follow roughly the proportionality rule (117). But with *Datura*, an increase from 2 to 4½ hours failed to result in an orderly increase in chromosome abnormalities, aborted pollen, or obvious abnormalities (22).

In *Habrobracon* "Shot" wing varies in degree and percentage with dosage, probably requiring a physiological explanation (299). The close relationship between the induced mutation frequency of *Drosophila* and intensity was determined by Hanson; the rate of induced mutations and the amount of ionization formed equivalent curves (95, 97). Proportionality holds true with variations in x-ray voltage (105, 107); and with variations in the duration of x-ray treatment (197, 200), the observed mutation rates approach the calculated percentages based on proportionality. Serebrovsky and Dubinin concluded that with dosage doubled the mutation rate will be doubled. Efroimson found this to be true for the three series studied, although the intensity required to produce a mutation may vary for the three. Intensity governs the mutation rate whether treatments are given continuously or intermittently (224), or whether two unequal radium intensities are given with time variations to produce equal total intensities (102, 103). Lacassagne and Holweck also found this to be true with yeasts. Packard (204, 205) made use of the biological effect as a measure of dosage.

Induced sterility in *Drosophila virilis* is not proportional to dosage. A rapid increase in sterility occurs near 2000 r-units if the females are treated (45).

Use of lethal mutations for gene mutation rate

It is probable that all lethal mutations are not point mutations, but that some are connected to, and due to chromosomal aberrations (168, 296), or definite deficiencies (227). Calculations indicate that approximately 25 per cent of the induced lethals are due to chromosomal irregularities (200). These lethals connected with chromosomal alterations do not increase in frequency in proportion to dosage, but increase rapidly with the heavy dosages (197, 200).

The F_2 lethal method used with *Drosophila* does not show all the induced mutations, but only the mutated chromosomes, due to chance grouping of mutations at higher dosages (61, 244). Grouping occurs for given dosages with the frequency expected as a matter of chance, if allowance is made for the lethals due to

chromosome breakages; also all F_2 lethals are found not to be lethals in the next (F_3) generation; however, this variation is about equal for the different dosages (200).

Relation of intensity to chromosome irregularities

That x-rays increase the frequency of inversions as well as lethal mutations in *Drosophila* has been reported by Serebrovsky (243), Muller (167, 168, 169, 170), and others. The direct proportionality of the frequency of induced sex-linked inversions and translocations for *Drosophila* was determined by Oliver (199, 200), and of deficiencies for maize by Goodsell and by Stadler (261). Non-disjunction occurs proportionally to the increase in r-units only for lower intensities (45).

Relation of wave-length to mutations

Through a wide range of wave-lengths, Stadler (258) found that x-rays are about equal in power to cause mutations in barley. Using *Drosophila*, Hanson (107) and also Gowen and Gay (80) concluded that it is a question of quantity rather than quality; but Efroimson using equal r-units (1000) for the different series studied found a slight variation in the induced lethal results. *Antirrhinum* is more susceptible to treatments of 30–50 KV than to harder or softer rays, as a consequence of the favorable conditions of absorption (277). Packard and Lauritsen in their measurement of *Drosophila* death rate found that different wave-lengths through a wide range are effective.

Natural radiation and spontaneous mutations

In the experimental results, no threshold dosage has been found below which mutations are not induced. It seems probable that if the intensity is carried to that of the natural (earth) rays, the mutation rate will be proportional to that intensity. Low (natural) intensities do seem to induce mutations proportional to the ionization strength. With two measured intensities, one double the other, Babcock and Collins (12, 13) found that the higher intensity induced mutations in *Drosophila* with a frequency just twice as great as that for the lower intensity (13 lethal mutations in 2500 cultures as against 9 in 3481). Radiations in a carnotite mine equivalent to a known radium test produced 7 lethals in 2860 test cultures to 1 in 1308 controls (99, 100). Both experiments suggest the possibility of the influence of natural radiations in the production of spontaneous mutations.

Calculations based upon the induced results obtained with *Nicotiana* indicate that natural radiation may account for the known spontaneous rate of mutations (203). If the gene mutation rate in *Drosophila* is considered, natural radiation can account for only 1/1000 of the spontaneous rate (182), nor is there sufficient radioactive substance in the organisms or food to account for the rate. Calculations of the ions needed for the production of one lethal mutation in the series studied by Efroimson also indicate that natural radiation is not sufficient to account for the rate in *Drosophila*. Due to the equal frequency of translocations and genes for a given dosage, Muller and Altenburg (179) concluded that the natural cause of mutations probably differs from x-rays in that the former produces more gene as compared to chromosomal mutations than do x-rays.

Agents active in production of mutations

The secondary or beta radiation was suggested by Muller (170) as the effective

agent in the production of mutations. Due to the close correlation of the ionization and the mutation-rate curves when superimposed, and since the beta particles do cause the ionization, Hanson and his coworkers (97, 105, 107) believe they have distinctly shown the beta particles to be the active agents in inducing mutations. In this they are supported by Timofeeff-Ressovsky (290); and Stadler (262) found that mutations may be produced by the beta rays of radiothorium and by cathode rays.

How agents produce mutations

Mutations are results of the direct action of x-rays. It is the position in the path of the rays rather than chemical composition that determines whether a gene mutates (170). This is shown by the fact that only one of a pair of allelomorphs is altered (170, 232), by the fractional effect from the treatment of sperm (170), by the independence of the degrees of change and dosage (170, 232), and by the direct proportion of mutations to dosage (173, 232). Muller (173) has found that transverse induction does not occur. Results offer no evidence of a delayed effect of x-radiation either in the subsequent generations (167), or in somatic tissues (173). If the directly induced lethal mutations in *Drosophila* are eliminated by proper matings, subsequent matings produce no "delayed" lethal mutations (87, 288, 290).

In the production of fragmentation, x-rays cause a degree of instability in chromosomes that is expressed only when the chromosomes come under the influence of energized cytoplasm (68). Although gene mutations seem to be due to immediate action, fragmentation apparently is due to a "post action" in the form of a durable chemical change in the plasm or chromosomes (128), and fragmentation is not due to a general condition within a cell, but to local combinations of conditions near the place of breakage. Patterson (231) concluded that part of the effect of irradiation on elimination of a chromosome may be indirect.

It may be that the x-rays do not induce mutations, but merely reveal a pre-existing latent state (46) or that they exert selective action upon the normal type (190, 191). To this Muller (176) does not agree. The mutational effect of x-rays upon mature sperm of *Drosophila* is permanent during the life of the sperm (108); and Muller (167, 168) believes that the death rate of mutated sperm is no greater than that of the unaffected. Harris found no correlation between the production of mutations in sperm and their viability.

About half of the induced mutants prove to be sterile. Muller (168) observed that with most mutants the germinal does not correspond to somatic tissue, i.e., the mutants do not breed true. Hanson and Winkleman investigated 204 visible mutations induced in *Drosophila* with radium; of these, 43 were germinal; 80 did not breed true; 81 were sterile.

Muller (173) believes that induced mutations for the most part are not a result of the destructive action (losses) of the x-rays. Those mutations induced are in part similar to the spontaneous ones; the proportion of lethals to visibles, or of dominants to recessives, is similar to that in the spontaneous rate (168, 173). The genes that mutate more frequently spontaneously, also do with x-ray treatment, and they are scattered along the chromosome in the same way (168, 108, 232). That known chromosome abnormalities and gene mutations are not one and the same thing is shown by the partial separation of the two conditions with sex (232).

All mutations are losses according to

Serebrovsky (243, 245), and Dubinin (59). According to Stadler the possibility is not excluded that the induced recessive mutations are merely absences of dominant genes, although the appearance and behavior of induced mutations are the same as the spontaneous ones. In barley, few if any dominant mutants are found (258, 262), and this suggests the possibility that special classes of mutations are induced. Deficiencies in plants are lethal to the gametophytes. In maize among the plants grown from treated embryos, only the defective plants have the new (dominant) characters; and these traits are not reproduced to later generations (262). Patterson and Muller (232) recognize that some mutations may be losses, and Patterson (227) found that x-rays do produce many definite deficiencies that in so far as they can be measured cover only a single known locus.

Some progressive, non-destructive mutations are produced by irradiation. Reverse mutations in *Drosophila* of scute and forked have been induced (170, 232) and have been shown not to be due to suppressors. Eight mutations of normal to forked and eight of forked to not-forked were induced with none in an equal number of controls (173, 232). In the latter case a mutation of a mutated not-forked to forked was reported, showing that the x-ray action is reversible. Somatic reverse mutations also occur; however, the rate is not as frequent as for the other direction (218, 283, 284). Timofeeff-Ressovsky also found reverse mutations for several loci on X and III of *Drosophila* (286, 287). Changes that breed true have occurred in cotton from recessive forked to normal leaf, and from virescent yellow to green (117, 118, 119). In sorghum the change from recessive virescent yellow to dominant green has occurred (Hor-lacher, Karper and Quinby, reported for 201).

Difference in susceptibility

Different loci in *Drosophila* vary in the frequency of induction (168, 170, 227, 286, 287). Patterson (227) connects this variation in some loci with the influence of deletions and viability genes. The frequency of deficiencies (loss of dominant genes) in maize varies for the different endosperm and plant genes tested (67, 261). Not only do different genes show a different mutation rate, but the rate varies for the same gene in different stocks (260). Timofeeff-Ressovsky (291) found in the induction of white and its allelomorphs that the Russian *Drosophila melanogaster* is more stable than the American. Whiting and Bostian (299) found different stocks of *Habrobracon* to vary in the production of "Shot" wing, as did Stubbe (275) in the production of variations in *Antirrhinum*, and Brittingham (27) in *Oenothera*.

The condition of polyploidy causes a variation in the frequency of response to irradiation. Oats and wheat with a basic chromosome number of 7 have a mutation rate equal to that of barley, but the frequency decreases with the increase in chromosome number (257, 258, 262). The lability of germ plasm after treatment is indicative of the evolutionary status of a species of *Nicotiana*, the species with the greater number of chromosomes having a greater variation of responses (70, 73, 74, 77).

Glass found in *Drosophila* that the regions of the autosomes nearer the spindle fiber are more likely to be fragmented by irradiation. Oliver (200) also reported a greater susceptibility of the right end of the X-chromosome, although this may be explained as due to the large bulk of inert material in this region.

Evidence as to composition and behavior of genes

Apparently a difference between the behavior of a gene in heterozygous and homozygous condition has been observed. When heterozygous agouti mice were subjected to x-ray, color was replaced by white; in homozygous agouti, by areas darker than the original. It is believed by Hance (91) that the heterozygous determiner is weaker and destroyed; the homozygous, stimulated to greater production.

In the analysis of the composition of the gene, evidence points to the fact that there are no gene elements. Mosaic tissue that sometimes occurs is not distributed in patch-work order; no "after effect" of irradiation is known; and most mutations are stable (167, 168, 170). At time of treatment, however, genes are compounded in the sense that only a part of a gene mutates. This is seen in the fractional effects induced. Fractionals are explained as due to the precociously doubled genes in the sperm, with only one daughter-gene responding to the treatment (167, 168, 170). Patterson (229, 231) found that mosaics from fragmentations do not appear after irradiation of female germ cells, although aberrant females do. He concludes from this and other results that the gametic chromosomes are not split in the eggs at the time of treatment, and that in the sperm the split has not always occurred.

Evidences of essential (viability) genes (24, 228) and support of the position-effect hypothesis discovered by Sturtevant in *Drosophila* have appeared in irradiation experiments (54, 58, 247).

Gowen and Gay (80, 82) used measured ionization and the mutations induced to determine the gene number and size in *Drosophila*. They found from calculations that there are at least 14,380 genes, each at least 1×10^{-18} cm^3 in size.

VII. USES OF IRRADIATION IN OTHER GENETIC PROBLEMS

Mechanism of crossing over, synapsis, and reduction

Induced exceptions have been used to substantiate evidence that crossing over occurs in the four-strand stage, and that assortment is determined at the spindle fiber end of X (7, 9). In the latter report, Anderson drew the conclusion that whatever decreases the intimacy of synapsis, especially near the right end of X, causes a decrease in crossing over and an increase in the amount of secondary non-disjunction. Dobzhansky's results (53) corroborate this conclusion.

The results found with translocations in *Drosophila* suggest that the point of spindle fiber attachment of III plays an important part in the distribution of crossing over (49), although crossing over need not begin first at the spindle fiber (66). Homologous rearrangements indicate a regional differentiation in crossing over. With the ruby-lozenge region of the X-chromosome moved nearer the spindle fiber end, crossing over occurs in that region with a frequency of one-third its previous value (195). Similar results with other alterations have been reported by Offerman and Muller (196). Beadle (18) found with a homozygous translocation that the spindle fiber interferes with crossing over in its immediate neighborhood.

In an investigation of reduction in translocation III–II, the point of fiber attachment seemed to have the greater weight in deciding the direction of migration, since no non-disjunction involving fiber-attachments occurred. However, with a large fragment attached to IV, non-disjunction of IV occurred more often due,

apparently, to its small size as compared to the conjoined fragment (175). Investigations of several translocations indicate that one factor determining the disjunction of involved sections is the relative length of these sections; the spindle fiber is a secondary factor (52, 53, 57, 278).

Synapsis and crossing over are due to an attraction between genes (homologous parts) rather than to the chromosomes as a whole (51, 53, 57, 170). Homologous parts tend to synapse even when attached to unlike parts that bear the spindle fibers (173, 183). This is observed especially in reciprocal translocations of *Drosophila*, in which the two large V-chromosomes have exchanged arms. Somatic pairing is never normal, but is characteristic for the attraction of like parts (57, 202, 278, 294). In maize, pairing was reported as that expected on attraction (152), although recent work seems to determine that at certain stages this is not true (153).

Since chromosomes are tenacious, attractions pulling in different directions (translocations) or the conflict of attracting forces (inversions) limit crossing over (51, 53). Beadle and Emerson have used combinations of heterozygous translocations, and from the results concluded that the reduction in crossing over near the point of fragmentation requires another factor than counter attraction as an explanation. Somatic pairing in *Drosophila* corresponds to the observed crossing over and corroborates the interpretation of Dobzhansky (51). If no crossing over occurs, the tendency is for the involved pair of chromosomes to show no attraction; if crossing over occurs only in one arm, only one arm pairs with its mate in the homologous chromosome (202, 294). Genetic investigations of the influence of translocations on crossing over have been made with homozygous and heterozygous aberrations. In all the intervals studied by Dobzhansky (47) in homozygous translocations, crossover values were but slightly, if at all, different from the standard values. Later, Beadle (18) did find some variation in the regions near the fiber locus. In the heterozygous form, crossing over occurs between the fragment and its normal homologue, but with a reduced frequency (170). In general, crossing over is decreased in the whole limb that is fragmented and increased in the other limb (53 and earlier). If the break occurs near the fiber locus, crossing over in the fragment may or may not be affected (51). Van Atta (294) and Glass found that such a break did not affect crossing over in either arm. The presence of a duplication of II (236) and of X (51) was found to decrease crossing over in the regions near the respective point of breakage even though otherwise a normal chromosomal configuration was present.

Mapping of genes upon chromosomes

The linear sequence of the genes in *Drosophila* as theoretically mapped is shown by the results with fragmentations to be correct. Genes involved in a translocation or a deletion constitute a coherent section of genes that corresponds to the fragment. However, the linkage maps do not represent the spacial relationship of the genes on the chromosomes. Crowded map regions are found to represent greater lengths cytologically; sparse regions on the maps are not as long physically in II and III (48, 49, 50, 51, 178, 183) or in X (55, 184, 212, 213, 214, 215). All the known genes in X except bb are found to be in about the left half of the chromosome, the right half being homologous to the Y-chromosome.

Mapping of chromosomes is made more definite by the use of irradiation. In the small IV of *Drosophila* the locus of ey has

been separated from bt by a fragmentation (24). The use of an induced translocation determined the pair of chromosomes in *Apotettix* responsible for the 13 factors for the dominant elementary color patterns (186, 187, 237). By a combination of the cytology and genetics of aberrations it has been possible to determine the regional location and the order of genes in maize linkage groups (152, 262).

Sex determination in Drosophila

Evidence that might offer some explanation of sex determination has been watched for in translocation and fragmentation work. That the left half of X is probably not sex determining was concluded by Muller and Altenburg (178). Certain duplications of X did not prevent males from breeding, and these regions were considered to be free of sex determiners (214). Suggestions of the use of duplications and translocations were referred to by Muller (173, 185). Evidence has also been sought in aberrant and gynandromorphic flies. Results by Patterson with special cultures indicate that a region near garnet may include a primary sex-factor, gene or genes (221, 223, 225); but in an investigation using intersexes, duplications of X were found by Dobzhansky and Schultz (56) to cause a shift towards femaleness, the longer the piece the greater the shift.

Variegated characters

Every known case of mottled eyes in *Drosophila* involves the locus of white and some kind of fragmentation with reattachment (24, 170, 173, 174, 226). Muller (173) does not believe that the variegated condition can always be explained as a loss. However, in one case, the fragment of X is attached to IV and apparently lost during somatogenesis. This mottling is interpreted by Patterson and Painter as due to an unstable translocation (226, 233). Gowen and Gay (81, 83) found evidence to support the conclusion that the Y-chromosome plays a part in mottling, as does also temperature (84).

The "eversporting" eyes are dominant and variegated, and continually mutate (170, 173, 174, 295, 296). All induced dominant eye colors are not variegated (198, 293, 294); but all observed variegated conditions are in some way connected with fragmentation of an autosome. Van Atta (293, 294) found the tested variegated mutants to be allelomorphs, located in the right region of II. Glass located three groups of allelomorphic genes for variegation, and found that variegation does not depend solely upon the connected fragmentation. Reversions of the visible mutation back to the normal type occur, but the translocations are retained. Morgan, Bridges, and Schultz (163) reported one mosaic to be allelomorphic both to light and to brown.

Maize endosperm mosaics are due in part if not in all cases, to the loss of a part of a chromosome (258), and within these areas are spots that show recovery or return to the dominant type. This recovery occurs in control as well as in treated material, and in spots with no internal connections (259, 261).

Oenothera problems

The tendency for the induced translocations in some cases to form the old, parent combinations, the occurrence of mutual translocations, the decrease in the frequency of crossing over in heterozygous translocations, and the presence of a lethal condition in most homozygous translocations are conditions that offer aid in the

explanation of the known conditions in *Oenothera* (57, 175, 278). Judging from somatic pairing when chromosomes of *Drosophila* have exchanged whole arms, rings probably are formed during maturation (57).

Variations in the dose of definite genes and of chromatin

One dose of purple (deficiency) produced no exaggerated effect (162). Muller found that an increased dosage of genes caused an increased phenotypic effect. If recessives are added, the effect approaches, or is greater than normal. These genes produce an effect like, but less than normal genes. On the other hand, bar and other dominants produce an effect different from that of normal (181). Dobzhansky and Sturtevant (58) found that the addition of the normal allelomorph in fragments does not suppress the action of a recessive gene as strongly as does the normal allelomorph in triploid condition. A similar condition was reported by Sivertzev-Dobzhansky and Dobzhansky. The explanation may be genetic balance or it may be position effect. A somatic cell in a *Drosophila* male that loses a piece of the X probably dies. This conclusion is based upon observed scars of the eye (218) and on the lack of gynandromorphic parts having only the lethal ClB combination (223). Chromatin added as a duplication generally is expressed by phenotypic variations, although not in all cases.

Other uses

Irradiation has been used to study the rôle and significance of quantitative chromosomal changes which are reflected in alteration of specific plant characters and to get self-perpetuating new lines in *Nicotiana*, differing from the untreated parents in external morphology (74, 75). Induced mutations have made the analysis of inversions less difficult (185), and an induced translocation has been used by Stern (271, 272) to aid in the cytological proof of crossing over in *Drosophila*. Variations in abundance occur with the proper irradiation of an organism. No method has as yet been reported by which the induction of the genetic effects may be controlled. It is possible only to irradiate and to accept the results produced, but each experiment presents new and interesting conditions.

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ON THE DYNAMICS OF POPULATIONS OF VERTEBRATES

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I

THIS paper is a summary of a more extensive work on the biology of reproduction of higher vertebrates. The latter work, which is forthcoming, is devoted to the comparative study of the growth of populations of the higher vertebrates. The statistics of the game in hunting grounds are practically the only source of information available about the dynamics of populations of birds and mammals. A clear concept of the biology of the forms studied is of course necessary for analyzing these statistical data, but in view of the briefness of this summary, attention is chiefly concentrated on the analysis of the curves showing the growth of the animal population. The description of the biology of the animals and examples illustrating the character of a very important phenomenon —the recurrent plagues among vertebrates—are also reduced to a minimum.

The analysis of the statistical data required the adoption of such a method of investigation as should give the possibility of estimating the trustworthiness of the figures and at the same time of ascertaining the relative importance of the single factors worked out in the course of evolution and determining the rate of growth of the number of animals of different species. I calculated theoretically the rate of increase in the numbers of animals on the basis of our knowledge of the fertility of animals as it is available in the literature, though this knowledge may not be very exact. I then compared the figures obtained theoretically with the figures representing the dynamics of animal population as observed in life.

Since the logarithms of terms of a geometrical progression form an arithmetical progression, I plotted the logarithms of the yearly registrations. In this way I could judge, by the closeness of fit of the points to a straight line, the exact measure of correspondence between the theoretical results and the reproduction of animals in real life. This method enabled me to show that the growth of the numbers of vertebrates in life actually follows the exponential curve, determined, for different species, by the species constants of reproduction (*Vide infra*) corrected for a definite value of the death-rate among the adults and among the young.

A preliminary communication about some questions studied here more minutely has been already published (S. A. Severtzoff, 1930). Endeavoring to determine the curve of growth of animal populations, I followed the path traced by ichthyologists studying in detail the age groups of different fish populations, whereas the majority of students of the growth of human population, as well as of the population of invertebrates easily reproducing themselves under conditions of laboratory life (*Drosophila melanogaster* and some other forms), are satisfied with the study of the growth of the population as a whole. It was found in many cases that the growth-rate of the population could be adequately

represented by the so-called Verhulst-Pearl logistic function,

$$y = \frac{k}{1 + e^{a+bx}}.$$

The logistic curve has the form of an *S*, showing that the absolute growth-rate increases slowly in the beginning of the period of growth, that it then accelerates, and that, finally, after a certain critical point of the density has been reached, it gradually decreases.

Pearl (1920–1923) showed that the logistic curve adequately describes the growth of human populations. His experiments with *Drosophila* have also shown that the increase in numbers in conditions of laboratory life attains the greatest rapidity in the case of an optimum density; in the case of a smaller or a greater density, the growth is smaller. We cannot see in the coefficients of Pearl's equation quantities having a biological significance. It is plain at the same time that there is nothing in common between different biological phenomena underlying the processes of reproduction of different forms, though they may be represented by one and the same curve. Chapman cultivated *Tribolium confusum* in a certain amount of flour. This flour was periodically renewed so that the quantity of flour might be sufficient for the population, but, while the number of worms increased, the rate of growth of the colony was delayed, because, together with the flour, the insects devoured the eggs laid in it.

A colony of *Drosophila* was bred in bottles of limited volume and in this case, as well as in the case just mentioned, the rate of reproduction decreased, while the population increased. The causes of the two processes being different, it is perfectly plain that both these cases have nothing in common with the growth of human population. The complicated social relations in conditions of class strife, the coefficients of death- and of birth-rates in different classes, the immigration and the emigration of the population and the relative development of the productive forces in different countries do not allow one to compare the growth rate of human population with the reproduction of animals without a special analysis of both. Thus we have to admit that, though the logistic function gives us the possibility of representing the growth of the population from its external aspect, it does not assist us in the understanding of the biological significance of the phenomenon.

The large investigation of Fisher appeared in 1930. Fisher put forward an index of growth which he called: "the Malthusian parameter." He examined the fertility and the mortality rate of different age groups and suggested an equation which allows one not only to calculate the growth-rate on the basis of given birth- and death-rates, but also to foresee its dynamics in future. Unluckily the method of Fisher cannot be applied to animals, as he proceeds in his calculations from the mortality tables used by life insurance companies and from birth tables derived in the same way. These kinds of statistical data are available for human populations, but they do not exist for animals.

The same year 1930 saw the publication of the work of Cholodowskij. The author considers only the mathematical aspect of the problems; he gives equations for the calculation of the number of animals, when the following data are known; the number of pairs of ancestors, the age of sexual maturity, the length of the period between two consecutive parturitions of the female, etc., i.e., the inherited characters, which we call the "constants of reproduction of the species;" he does not take into consideration the mortality of

the animals, which is reducing the potential growth of the population.

Pearl's (1926) so-called "vital index" is evidently largely recognized by demographers studying the growth of human population. This index determines the growth of the population of a given country by the ratio of the births (B) multiplied by 100 to the deaths (D). When the figure exceeds one hundred it means that the population is increasing, when it falls short of one hundred it means that it is decreasing. The difference between the fertility of man in different countries and the fertility of different species of vertebrates is so great that it is not possible to apply methods worked out for the human population, when we have to compare the fertility of different species, and in order to be able to make such a comparison I had to work out a special index of fertility of species.

I dealt in my paper of 1930 with the following questions: what are the factors determining the growth rate of the population of different species; what is the curve formed by the growth of the population, and what are the factors delaying or interrupting the growth? The index of species fertility which I suggested—q—allowed one to characterize, in a first approximation, the relative fertility of different species in so far as this fertility depends on the inherited characters of the individual.

In life we always have to do with the reproduction of a certain number of individuals forming a herd, this reproduction going on for several years. In the case of the majority of vertebrates the parents are still living when their young have attained the age of maturity and are breeding in their turn. Thus the herd is composed of several age groups. Every year a certain number of the individuals of each group perish and the diminution of each age group is compensated, as a rule with some surplus, by individuals of the next younger age group. Thus the age composition and the curve of increase in numbers are determined by the birth- and death-rates of the age groups composing the population.

We shall begin by considering the rate of reproduction of vertebrates (without first taking into account the mortality of animals) and we shall try to compare the potential fertility of different species. (My conception of the potential of fertility nearly approaches Chapman's conception of the biotic potential, which he proposed some time ago, but which was unknown to me till the year 1933. However I prefer to retain the term "the potential of the fertility of species" because as it seems to me, it expresses my idea more clearly and more adequately.) Each herd reproduces itself according to the rate of individual development and the fertility of the individuals forming the herd, and we have to trace how far the characters of the individual are manifested in the fertility of the herd.

The potential rate of increase of the herd depends upon the inherited characters of the individuals of each species, which may be called constants of reproduction of the species; these constants are just as characteristic of the species as its morphological characters. Such constants are the following, calculated by the method of variational statistics: the number of the young produced every year by one pair (r); the age of the first parturition, i.e., the age of sexual maturity plus (for mammals) the length of the period of pregnancy (j); the period between two consecutive parturitions of the female (p). The relative number of the sexually mature males and females in the herd and the percentage of barren females have, so it seems, only a secondary importance and the deviation from equality of the numbers of males and females, in the case of vertebrates, is

hardly determined by heredity. A theoretical curve of the increase of the herd can be drawn for each species when the above named figures are known. Several curves calculated from the formula of Cholodowskij (1930) are given in figure 1. Examining them we see that the rate of growth of the herd is determined in the first place by the number of young produced by the female every year (r), the increase of the herd being the more rapid, the greater the value of r (Curves j_3r_3, j_3r_4, j_3r_5). When r is constant the reproduction of the species is slower, the greater the value of j (j being > 1 year). The rate of growth is still slower when the females do not bear every year, but at longer intervals of time, for instance once

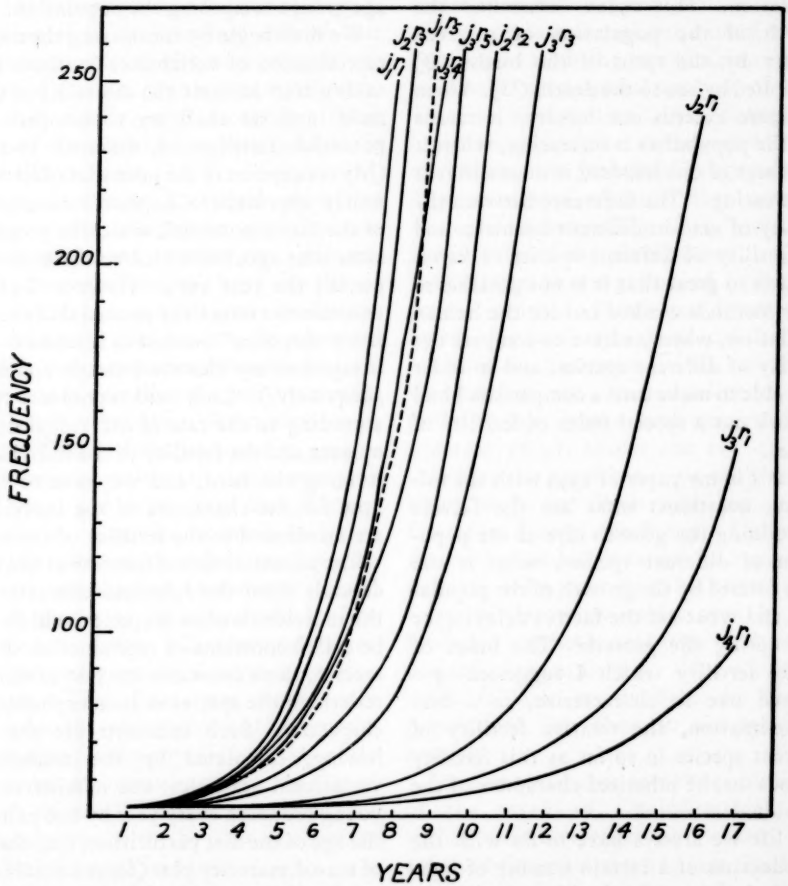

FIG. 1. THEORETICAL CURVES OF THE INCREASE OF THE HERD, FOR DIFFERENT VALUES OF THE SPECIES CONSTANTS

j = age at first parturition, r = number of the young produced by the female per year. The curves show that the rate of increase is accelerated with increasing r and reduced with increasing j.

in two or three years. The retardation of the growth of the herd, when p has a value greater than one year, is proportional to $\sqrt[p]{r}$.

Examining the curves of figure 1, we find that the difference between the course of the curves r_1j_1 and r_1j_2 is considerably greater than the difference between the course of the curves r_1j_2 and r_1j_3, and that this difference is entirely due to the value of j in this interval. The comparison of the curves of potential fertility of the herd brings us to the conclusion that the different species of vertebrates can be arranged according to their fertility in a very regular sequence, not only the number of young, but also other constants of reproduction of the species being of importance.

The growth rate of the herds of two different species may be the same, although the number of young borne by the females of these species be different, if the constants of reproduction j and p have corresponding values. Now we can express the index of the species fertility (q) by the equation

$$q = \left(1 + \frac{r}{(F)j}\right)^{\frac{1}{p}}.$$

where $Fj < j$. The exact function of j (Fj) was not ascertained by us, but the examination of the curves shows that $Fj < j$. Still we may use j, as the changes in Fj correspond to the changes in j. Introducing into this expression the values of the figures for the constants of each species we can characterize the fertility of one species in relation to another by one figure.

We have to note here that from the point of view of the biology of reproduction of the herd the constants j and p are not only temporary categories, as they appear to be at first sight, but, together with the percentage of the barren females and the relative number of the individuals of different sexes, they represent the coefficients determining the number of those individuals in the herd that are not bearing every year. The individuals not bringing forth any issue in the given year, either because they have not yet attained the age of sexual maturity or because they have bred the year before, still go on living in the herd; together with the others they use up the food supply of their habitat (*Wohnraum* of German authors) without taking part in the reproduction of the herd. The yearly reproduction of the herd evidently depends upon the number of the bearing females alone and this number may be greater or smaller according to the value of j and p.

I showed in my work of 1930 that the duration of life of the individuals, as characteristic for the species, stands in an inverse proportion to the logarithm of the index of the species fertility q. The fertility of the species decreases with increasing duration of life not only at the expense of the reduction in the numbers of the young produced by the female, but also in consequence of the rise of the values of j and p, that is, in consequence of the reduction in the numbers of bearing females in the herd.

However, we cannot confine ourselves to the comparison of the potential fertility of different species, the growth of the herd of any species in nature being reduced by the mortality of the individuals in their struggle for life. In accordance with A. N. Severtzoff (1917) we may distinguish the mortality of the young individuals, sexually immature, and the mortality of the adult animals, the age of sexual maturity representing the limit after which the young animals generally attain the full development of the characters distinctive of the species. The reproduction of the animals is subject to a yearly cycle and generally falls in the spring and summer period of the year. According to the

length of the period of gestation and of the development of the egg, some species bear in the summer of the same year, when they have attained sexual maturity, while other species, with longer periods of gestation, having attained sexual maturity in autumn, bring forth a brood in the summer of the following year—e.g., the reindeer, the horse and other species, where the period of gestation lasts 9 to 11 and more months. Therefore, examining the growth-rate of the herd I think it preferable to take into consideration not the age of attained sexual maturity, but the age of the first parturition of the female, i.e., the age of attained sexual maturity plus the length of the period of pregnancy. This is in so far preferable as it is exactly the moment of the birth of the individual, which is of importance for the course of the geometrical progression of reproduction. Thus we shall distinguish the mortality of the young animals for the period j from the mortality of the adults and designate it by the letter m.

We can distinguish in the total number of any species three groups of different ages: (1) the sexually immature individuals, born in the given year or earlier; (2) the adult and breeding individuals forming the main group of the species; and (3) the old individuals which have outlived the period of activity of the sexual glands and are unfit for reproduction. If we examine only the growth of the adult group, which is increasing at the expense of the young group, having outgrown the period of mortality in the early age, the coefficient of mortality introduced by us will be equivalent to the decrease in the numbers of the new-born young. Therefore the curves of Figure 1 may be considered as showing the increase in the numbers of adult individuals out of whose brood the number $r_1 = r - m$ attain the age of first parturition (where $r > m$).

If the yearly fluctuations of the mortality of the young are not considerable, they evidently cannot change the character of the curve of the potential growth of the herd and transform the exponential curve into a logistic one. Such a change might take place only in the case where the increase in the mortality rate among sexually immature young or among the adults was progressing according to the growth of the population or in the case of a corresponding increase of the birth rate. Further investigations must show whether such phenomena take place in the life of vertebrates.

We possess hardly any figures characterizing the mortality of the adult individuals, but we know that it is subject to violent fluctuations and that there are years when it acquires the character of a mass plague. A series of observations leads to the conclusion that the periodic mass plagues are not an accidental, but a regularly recurring phenomenon dependent upon periodic changes in the external environment of the animal. Different species react differently to the same changes in their environment, according to peculiar characters of their constitution and their biology, as they have been worked out in the course of evolution. Fur-trade statistics and direct observations of the number of different species in nature have shown that there are years when the number of animals abruptly decreases and that it then gradually rises to the former level (Turkin, 1900; Elton, 1927). These declines are not brought about by man, interfering with the conditions of life of the animals, but by natural causes.

We have to look for the causes of the plagues in the first place to violent deviations from the optimum of the climatic conditions, acting sometimes directly, sometimes indirectly. The climatic elements vary about a certain mean, extreme

deviations occurring more rarely than slight ones. An extraordinarily deep snow in winter, covering the green herbage, results in the starvation and death of herbivorous animals. Snow-storms, glazed frost, inundations, droughts, prairie- and forest-fires, dearth of pasturage increase the mortality directly or indirectly and bring about mass plagues.

It is not always absolute deviations from the optimum of one of the climatic elements that are of greatest moment for animals, but often certain combinations of these elements, which can hardly be detected by meteorological stations of the ordinary kind; thus a plague may be caused in winter time by a comparatively slight fall of temperature, after a thawing of the snow and a rain, when the ground is covered by a hard ice-crust which prevents the animals from grazing. A plague among the herbivores naturally deprives the carnivorous animals of food and they die of starvation. Different species react differently to changes of climate and other factors in their environment, and a depression which means death for less resistant animals can be borne comparatively well by more resistant ones.

Another essential category of causes bringing about plagues among animals is epidemic diseases. A pest epizootic in the nineties caused the death of 90 per cent of the ungulates in Africa. We know of anthrax epizootics among reindeer, of coccidiosis and helminth infections among rodents and ungulates. In so far as infectious diseases resulting in plagues are brought about for each species by specific bacteria, protozoa, or helminth parasites, we have to admit that the agent of the disease always exists in the host population and that in certain conditions, increasing the possibility of infection of healthy individuals or reducing the resistance of the host in relation to the parasite, the disease spreads widely and can attain the character of an epidemic.

Direct observations have shown that a rainy summer with its many pools inhabited by *Limnaea stagnalis*, the intermediate host of *Fasciola hepatica*, contributes to the infection of hares, reindeer, sheep and some other herbivorous animals by the larvae of this parasite. When the same climatic conditions have caused an under-feeding of the game and thus reduced its resistance and its capacity to withstand the parasite, a violent infection will bring about an epidemic plague. When the number of animals of any species has reached its peak during a favorable period of the summer half-year, the food being sufficient and more animals being able to live on the same space, or during a period of several consecutive favorable years and when after this the conditions change for the worse, the numbers of animals prove to be so great that the conditions of life for each individual also change for the worse. The individuals cannot resist the disease and the density of the population itself contributes to the infection.

For the majority of rodents we are able to establish a regular periodicity of epidemic plagues from infectious disease, following on a mass reproduction of animals. The same periodicity has been established by Elton (1927) for predators preying upon these species. However, at least according to fur-trade statistics, such a regular periodicity could not be traced in relation to ungulates and less fertile rodents (*Castor fiber*). Nevertheless what has been said above about recurrent violent deviations of climatic factors from the average and about epidemic diseases forces us to admit that all species are, from time to time, subject to plagues, but that the frequency of these plagues must be different according to differences in the constitution and in the biology of the species.

There is one more point of great moment, which has to be considered. Plate (1913) is right in pointing out that plagues caused by abiotic factors are not connected with the density of the population; a sparse population may perish from inundation, glazed frost, or dearth, just the same as a dense one. Therefore, insisting upon the fact that the resistance of different species is different in regard to the same changes in their environment, we think that within the limits of the same species extreme deviations from the optimum exceed the endurance of individuals to such an extent that their individual characteristics lose their importance and survival is subordinate to the law of great numbers. Therefore the greater the number of individuals forming the population of a locality before the breaking out of a plague caused by abiotic factors, the greater will be the number of individuals surviving the plague, and the more certain the restoration of the level needed for enabling the species to survive the next coming depression. If any of the species does not succeed in restoring its level a still smaller number of individuals will survive the next coming depression and the species will die out.

We have laid stress on abiotic factors of the plagues because the conditions for the possibility of surviving depressions caused by abiotic factors require the highest possible population. A dense population is a factor favorable for the spreading of epidemic diseases which also destroy the population according to the law of great numbers, although this density is not the only cause of diseases. We hold that the fertility of the species must correspond to the statistical recurrence of fluctuations in abiotic factors dangerous for the species, but in cases when the next depression is late in coming and the population has reached its highest density, there appear conditions favorable for the development of epidemic diseases. This fact must lend to the periodicity of epidemic diseases a greater regularity.

Direct observations on the periodicity of plagues show that some species are subject to them more often than others. From what has been said above about the potential fertility of animals and about some species being so much less fertile than others, it follows that if the frequency of the plagues caused by epizootics or by extreme deviations of climatic factors from the optimum were the same for fertile species as for infertile ones, the less fertile species would not have time enough during the favorable period for the restoration of their numbers reduced by the plague; therefore in a comparatively short time these species would disappear from the face of the earth. This shows the utter impossibility of admitting a simple periodicity in the mass reproduction of different species, connecting it with the periodicity of climatic fluctuations, resulting from the 11 year cycle of sunspots, as is done by Elton (1927).

As has been observed for many species, the coefficients of the periodic reproduction and of the dying off of the population must be specific for each species and must correspond to the potential fertility and to the mortality rate of that species between two plagues. We can gain knowledge about the rate of growth of the herd in the periods between two plagues only by studying the actual increase of the animal population in nature. Holding it necessary that specific investigations should be organized chiefly in national parks, we think nevertheless that, although the data already accumulated have been gathered with a different purpose and although they are not always sufficiently precise and complete, it is still possible to use them in order to make an attempt to

approach the question of the dynamics of a herd of vertebrates.

II

We are in possession of some statistical data left from the former imperial hunt in Gatchino near Leningrad, concerning the number of five species of game of the grouse family (Tetraonidae) and also the number of roes (*Capreolus capreolus*), these data recording the results of the hunting and of the struggle with predators for a period of 25 years—from 1886 to 1909. A report on these statistical data was presented by the chief administrator of the hunt, Dietz, at the Second Congress of Hunters in 1909 and they were published in the *Proceedings* of the Congress, but unluckily without the explanatory notes. The gap has to be filled up by desultory indications of Dietz, made at the Congress, and by some material drawn from the literature on the subject.

The imperial hunting grounds extended over more than 200,000 hectares and were carefully guarded against poaching, any unregistered shooting being thus excluded. The percentage of the game shot in the hunting grounds is very low. At the same time the curves representing the numbers of the birds of prey which were shot show a permanent increase due to the growth of the numbers of the game; thus we see that in the Gatchino hunting grounds the natural correlation between the predatory birds and mammals and their prey and also the standards of the reduction in the numbers of the game in its struggle for life were not seriously upset.

The use of the statistical data concerning the quantity of game in Gatchino presented a certain difficulty since the data included only the following points: the number of the young in each nest for each year, for all species taken together, and the total number of the young. I had therefore to calculate the number of the young for each species separately on the basis of the average number of the young in the nest, correcting the figure obtained for the fertility of each species. After summing up, for verification, the number of the young of each species, I compared the figures obtained with those given by Dietz and found the difference to be 1 to 2 per cent. Taking into account the degree of precision attainable by the registration, this difference may be considered unimportant. The number of breeders and the figure for the young being known for June and July of each of the 25 years I could calculate the yearly percentage of growth in the number of breeders, the percentage of survival and of the reduction in the numbers of the young for the winter period and, finally, Pearl's vital index; the number of the eggs laid by each female and consequently the number hatched not being given, I had to adopt for this number the number of the young in summer with the subtraction of the figure for the game shot. These calculations were made for the capercailyes (*Tetrao urogallus*), for the black grouse (*Lirurus tetrix*), the heathcock (*Tetrastes bonasia*), the ptarmigan (*Lagopus* sp.), the partridge (*Perdrix cinerea*) and the pheasant (*Fasianus colchicus*). All these birds are non-migratory and very slightly nomadic. This gave me the certainty that the figures obtained showed the real mortality rate and not the result of migration from the territory. Tracing the fluctuations in the numbers of these birds during a period of 25 years I could note a series of peculiarities in the reproduction of each species, but I shall give here only the description of the growth rate of the herd of partridges, and in part of the capercailyes.

In Gatchino the partridge was the most numerous bird. It is a very fertile bird, laying from 15 to 24 eggs. The young

partridges build their nests in the spring of the first year of their life and both parents take care of the brood. The growth of the herd can be easily followed in Figure 2 and Table 1. The number of birds for the summer of each year is represented by a column, the black part corresponding to the number of breeders and the other part to the number of the young brood at the moment of the registration (about June or July). The shooting of the partridges in Gatchino was not considerable; it amounted to only 6 per cent a year and could not affect sensibly the number of birds. We see that the number of partridges was subject to very great fluctuations. The young birds, registered one summer, passed in the spring of the next year into the group of breeders; thus the increase in the number of breeders was determined by the number of birds surviving the winter. The percentage of the surviving young birds appears to be very constant; we determined it as the ratio between the number of the young of the preceding year and the increase of the adult birds of the following year, when the birds, having survived the winter, began to breed in their turn. From year to year the percentage of survival was 5 to 6 per cent of the total number of the young bred during the summer minus the birds shot; this secured the increase of the breeders in favorable years to the amount of 28.4 per cent. The reduction in the numbers of the young brood during the winter was rather less as obviously there also perished a certain number of the old individuals. This latter number is unknown to us but in some measure it in-

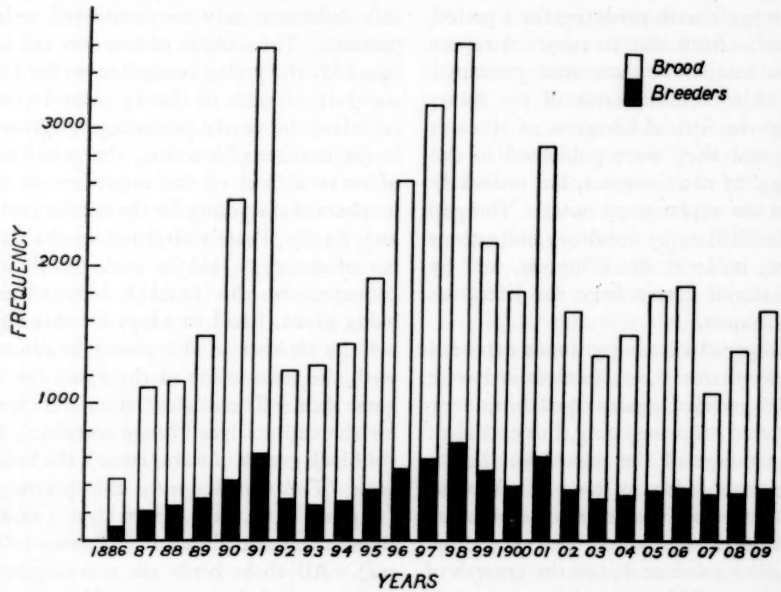

FIG. 2. DIAGRAM OF THE DYNAMICS OF THE HERD OF PARTRIDGES (PERDRIX CINEREA) IN GATCHINO FOR THE YEARS 1885–1909

Each column represents the number of birds in the summer of the corresponding year

creased the percentage of the reduction in the numbers of the young. The reduction in the number of the whole herd was 70 per cent on the average. The reduction in the numbers of the brood in winter, as taken together, was considerably reduced. We can trace a perfectly regular increase in the number of the breeders during six years, then an abrupt decline during two years, the decline in the second year

TABLE 1

Dynamics of the Herd of Partridge, Perdrix Cinerea, in Gatchino

YEARS	NUMBER OF BREEDERS ♂ + ♀	NUMBER OF YOUNG FOR THE SUMMER	GAME SHOT IN PER CENT	MORTALITY IN THE HERD — GAME SHOT	SURVIVAL OF THE YOUNG FOR THE WINTER IN PER CENT	MORTALITY OF THE YOUNG FOR THE WINTER IN PER CENT	GROWTH AND REDUCTION OF BREEDERS IN PER CENT OF THE NUMBERS OF PRECEDING YEARS
1886	104	363	14.3	—	—	—	—
1887	226	903	1.4	40.0	39.2	60.9	+117.0
1888	258	896	1.2	75.2	3.1	97.0	+14.0
1889	314	1198	10.8	72.1	6.8	93.2	+22.0
1890	454	2043	3.8	68.1	12.0	88.0	+45.0
1891	646	2968	2.6	71.0	9.8	89.2	+43.0
1892	302	950	3.5	94.5	0.0	100.0	−53.0
1893	268	1010	5.8	76.0	0.0	100.0	−11.0
1894	314	1122	0.2	70.3	4.8	95.2	+17.0
1895	390	1534	5.8	72.5	6.8	93.2	+24.0
1896	540	2111	5.9	67.4	10.3	89.7	+38.0
1897	600	2604	6.4	72.7	3.1	96.9	+11.0
1898	714	2934	3.4	72.5	4.6	95.4	+19.0
1899	552	1698	11.9	96.8	0.00	100.0	−25.0
1900	422	1421	7.1	71.7	0.00	100.0	−19.0
1901	636	2286	7.3	60.0	1.62	98.4	+50.0
1902	380	1315	6.7	81.3	0.00	100.0	−40.0
1903	332	1031	3.1	75.5	0.00	100.0	−12.0
1904	348	1181	9.6	72.3	1.6	98.4	+5.0
1905	394	1424	—	67.0	4.3	95.7	+13.0
1906	410	1499	13.5	77.4	0.00	100.0	+4.0
1907	288	921	17.3	68.5	0.00	100.0	−30.0
1908	360	1048	3.6	40.2	9.5	90.5	+25.0
1909	390	1312	—	70.0	29.8	70.2	+8.0
Mean.....			6.3	71.8	6.45	97.2	

Mean growth in the numbers of breeders for the years of growth = 28.4%
Reduction in the numbers of breeders
(a) for the first years of the plague = 39.0%
(b) for the second years of the plague = 14.0%

calculated by me, was as much as 90 to 95 per cent for the years when an increase in the number of breeders could be observed. The examination of the diagram shows that there were years when the number of the whole herd, old and young individuals being somewhat less than in the first; after this comes a second period of six years of regular growth in numbers and a new decline followed by a comparatively inconsiderable increase in numbers during three or four years, then again declines on a

smaller scale than the two first ones. It is evident that we have to do here with a periodic mass reduction in the number of birds, but no explanation of its causes is to be found in the records of the Gatchino hunt.

However, the knowledge of the biology of the partridge shows that these birds perish in large numbers during a severe winter and that besides they suffer from epidemic diseases and helminth infections. Unregistered shooting and lawless extermination of the game were excluded in the conditions of the Gatchino hunt, therefore we can admit only natural causes of the plague. Our attention was arrested by the fact that the reduction in the numbers of the herd went on for two or three consecutive years, (except, perhaps the year 1900) (Fig. 2). A plague caused by abiotic factors could last only through one winter but if the cause of the plague were disease or infection by parasites, the effect of these causes could last through periods exceeding one year's cycle, stopping only when the population had attained the sparseness necessary for preventing the parasites from attacking the healthy individuals too easily. A minute comparison of the fluctuations in the numbers of game with meteorological records of the chief geophysical observatory did not give any positive results.

Concerning the plague of 1900 I have some doubts, seeing that after the reduction in numbers of that year there was a very large percentage increase of the breeders. The old birds that had passed the age of breeding were evidently not registered; meanwhile it often happens that young birds perish in large numbers as a result of the spring frosts; while older ones safely survive them. We have thus come to the conclusion that the reduction in the numbers of the breeders in the year 1900 was only an apparent one.

Pearl's vital index of the partridge is very characteristic for this fertile bird; it proved to be $100 \frac{B}{D} = 107$ on the average for 23 years. Leaving out the first and the last year we have $100 \frac{B}{D} = 101.2$ or an almost total absence of any growth, although in the intermediate years the increase of the number of birds was very great (from 1000 individuals to 3600).

We can also note a very interesting coincidence between the five or six year periodicity in the increase of the numbers of the partridges with the duration of life of this bird, which, according to Mitchell (1911) attains seven years.

From the regular disposition of the logarithmic points showing the yearly number of the breeders, we can see how regular was the rate of reproduction of the partridges. On Figure 3 the years are marked along the abscissa, the logarithms of the numbers of the yearly registration along the ordinate. The regular disposition of the points shows that the growth of the population followed the exponential curve determined by the species constants of the partridge, corrected for the mortality rate for the first year of life, which for the partridge coincides with the age of the first production of young by the female. The mortality of the young was as high as 90 per cent. Examining the disposition of the logarithmic points on Figure 3 we see that the points of the ascending as well as those of the descending range are disposed with more or less regularity on straight lines. This alignment shows that the reduction in the numbers of birds also regularly followed a negative exponential curve. What is the reason for that reduction? If the increase of the mortality rate had been caused by climatic factors, for instance by a very severe and snowy winter, we could expect to find an abrupt

decline in the numbers of birds during one winter but, this cause ceasing to act the next spring, the number of birds ought to have again increased. The disposition of the points indicates a cause acting for more than one year. Volterra (1928) points out that the decline in the numbers of herbivorous species as a result of encounters with predatory species follows a descending exponential curve. He includes under predators the agents of diseases. The simplest explanation of the periodic plagues recurring among the partridges is the helminth invasion. The proved to be very near the figures which we had obtained for the partridges; periodic plagues were observed for other birds as well with the exception of the capercailyes (*Tetrao urogallus*). During the whole period of 25 years there was not a single considerable decline in the numbers of the capercailyes, but the growth of the herd of this species proved to be much slower than the increase in the numbers of partridges. Without entering into a closer analysis of the increase in the numbers of capercailyes, suffice it to say, that the duration of life of this bird is consider-

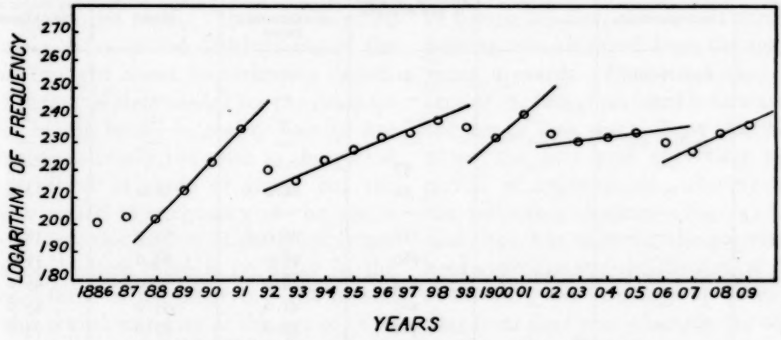

FIG. 3. THE PARTRIDGE (PERDRIX CINERREA) IN GATCHINO

The years from 1886–1909 (25 years) are marked on the abscissa. The logarithms of the numbers of breeders are marked on the ordinate. The regularity of the disposition of the points in relation to the straight lines shows the regularity of the yearly growth, interrupted by periodic plagues.

frequency of the encounters between the predatory birds and their prey causing the infection of the healthy individuals is a function of the number of partridges, therefore the frequency of the infection and the mortality rate must decline with the reduction in the numbers of the herd. This is exactly what happens in reality. In the first year of the plague there perished on the average 40 per cent of the whole number of breeders, in the second year only 14 per cent.

The index of survival and the mortality rate of the young for other species of birds ably longer. According to Brehm it has been known to live in captivity for 20 years. The capercailye attains sexual maturity at a considerably later age than the partridge. It begins to build nests and puts on the definite male attire of an adult cock in the third year of its life; the female lays fewer eggs than the partridge, from seven to nine on the average. In accordance with the smaller value of r and the greater value of j the reproduction of the capercailye goes on at a slower rate, and in accordance with the duration of its life it needs a longer period of time

for populating its habitat. The partridge reproduces itself more rapidly; the resistance of the individuals being less, the plagues and the frequent exterminations of the population are compensated by the fertility of the birds. At the same time the mortality rate of the young is practically the same for the two species of birds (90–95 per cent of the yearly brood).

Not only birds but also roes (*Capreolus capreolus*) were bred in the Gatchino hunting grounds. The results of this breeding are of great interest, representing as they do an extremely rare case of the reproduction of a large mammal during a period of 12 years (from 1895 to 1909) without any shooting and under supervision of the increase of the herd, left to natural conditions in its struggle for life. In the course of the 12 years the herd increased in numbers from 59 to 1068 individuals. The roes, which formerly did not exist in Gatchino, were imported from Germany to the number of 18 males and 19 females; three bucks and six does were supplied from the Oural and two females and one male from the Caucasus; much later, in 1907, three does and three males were brought from Atchinsk. In the beginning the roes were kept in an enclosure. In 1892 forty-one of them were let free into the forest; the data not being available for the years 1893, 1894, 1895, we have to consider the year 1896 as the first year of reproduction, their number being then 59. The roes in Gatchino, as in all hunting grounds, were registered by tracks left by them in the snow, generally in November or December, when the young, born in April and May, were seven or eight months old, and the first period of the juvenile mortality was over. On an appointed day all guards came out for the registration of the numbers of animals,

TABLE 2

Dynamics of the Herd of Roes (Capreolus capreolus) in Gatchino

YEARS	NUMBER OF THE ROES IMPORTED INTO GATCHINO	GAME SHOT	NUMBER OF ROES IN THE FORESTS	GROWTH OF THE HERD IN PER CENT OF THE NUMBERS OF PRECEDING YEARS	SURVIVAL OF THE YOUNG IN PER CENT	MORTALITY OF THE YOUNG FOR THE PERIOD "*j*"
1892	20♂ + 21♀	—	41	—	—	—
1893	—	1	—	—	—	—
1894	—	—	—	—	—	—
1895	3♂ + 6♀	—	—	—	—	—
1896	—	—	59	—	—	—
1897	—	—	72	22.0	30.0	70.0
1898	—	—	—	—	—	—
1899	—	1	127	76.0	64.0	36.0
1900	—	—	160	26.0	61.0	39.0
1901	—	—	204	28.0	57.0	43.0
1902	—	—	287	41.0	55.0	45.0
1903	—	1	321	12.0	27.0	73.0
1904	—	1	425	32.0	64.0	36.0
1905	—	—	498	15.0	28.0	72.0
1906	—	—	635	27.0	57.0	43.0
1907	3♂ + 3♀	1	755	19.0	35.0	65.0
1908	—	—	872	16.0	29.0	71.0
1909	—	6	1068	23.0	48.0	52.0
Mean					46.0	54.0

each forester counting up the incoming and outgoing tracks in his own district, the total number of the animals in the hunting grounds was calculated according to these data.

The following peculiarities of the roe should be pointed out here. The roe mates in August and the female bears kids in May, the period of gestation lasting nine months. We observe in this case a very peculiar development of the embryo, the egg passing very rapidly through all the stages of division and its development stopping after this for several months, while the formation of the fetus begins 4½ months before birth. Thus we have an obvious delay in the development of the fetus brought about by unknown causes. The period of time needed for the development of the fetus—in reality four to five months—is nearly the same as the period of gestation of sheep or goats, but the whole period of pregnancy of the roe is nearly the same as that of the much larger reindeer, where there is no delay in the development of the embryo. The female attains sexual maturity at the age of 15 to 16 months; at the age of two years she brings forth generally two, rarely three or one kid. According to German observations 20 per cent of the total number of adult females remain barren. The male attains the full development of his horns at the age of three, but sexual maturity sets in earlier, at the age of two, as is the case of the females. However, in so far as at the time of mating the males are fighting for the females, the young roebucks have a chance of partaking in the act of fertilization only in the case of scarcity of the adult males. According to German data the roe ceases to mate at the age of 10, but lives up to the age of 14 or 15 years.

The statistical data for Gatchino do not give us any information as to the number of the age groups forming the herd, but it is evident that the total number of the roes as given in these data includes the adults of two or more years, the young above one year, as well as the brood of the year minus those that had perished before the moment of registration, the analysis of the registration showing that the subsequent mortality of the brood was not great. I calculated theoretically the growth rate and the age composition of the herd of roes, starting in my calculation from two pairs of adults, the conditions given being the following: parity in the numbers of males and females, 20 per cent of barren females, the rest of the females bearing two kids each from the age of two years upwards. I assumed that 50 per cent of the brood perished before attaining the age of two years, those that had survived the first year surviving also the period of registration. Having plotted the following diagram (Fig. 4) I noted that the curve showing the growth of the herd approximates the theoretical number of breeders and yearlings up to 1903, but that from that year onwards the observed reproduction of the herd fell far behind the theoretically obtained figure.

Comparing this fact with the very low figures of the brood I assumed the slow increase of the growth to be the result of the mortality of the young in the year 1902–1903. The point which in my calculation represented the number of the yearlings was placed so that it corresponded to the point representing the real number of the Gatchino herd and I noted a further coincidence of the figures for the growth obtained theoretically with the empirical curve. This coincidence convinced me that the yearlings that had survived the period of juvenile mortality were really included in the registration, as well as all the other ages; this also encouraged me to calculate the rate of the total increase in

the numbers of the herd, basing my calculations on the constants of reproduction as indicated above, and assuming such a reduction in the numbers of the brood for the first year of life that the total number of the roes was equal to the number shown in the statistical data of the Gatchino hunt (Fig. 5). After having obtained these figures for the herd I further calculated the mean percentage of reduction of the brood. It proved not to exceed 54 per cent a year. In so far as a certain mortality, the amount of which is unknown to us, certainly took place among the adults, the figure for this mortality may be safely included in the 54 per cent mortality of the brood and the 20 per cent of the barren females. We are deprived of the possibility of determining the rate of reduction in the numbers of the adults, but we have to assume that the mortality rate of the brood was about 50 per cent of the number of the young born every year.

I showed in my work of 1930 that the mortality rate of the young during the

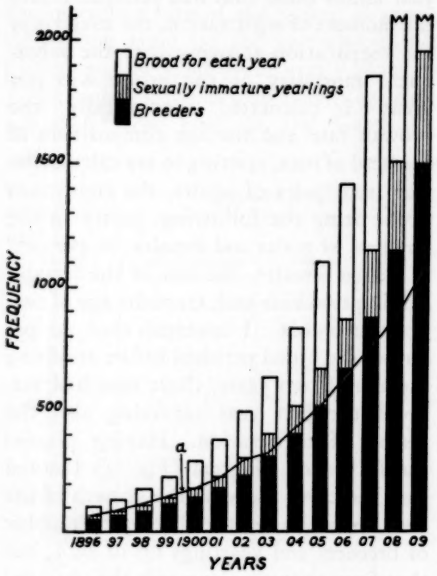

FIG. 4

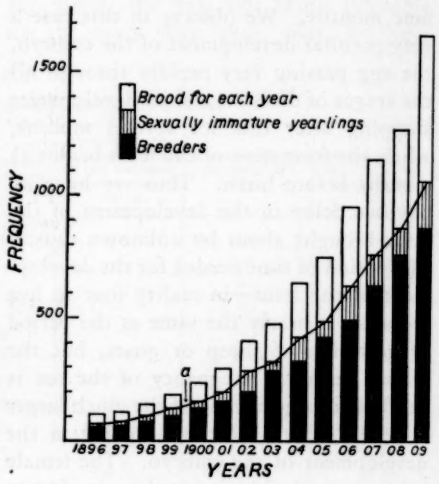

FIG. 5

FIG. 4. GROWTH OF THE HERD OF ROES (CAPREOLUS CAPREOLUS) IN GATCHINO

The curve *a*, representing the observed population, is drawn on the diagram of the growth of the herd of roes, calculated theoretically on the basis of the species constants of reproduction: $r = 2$, $j = 2$, $m = 50$ per cent of the new-born young. Initial population = 59; every year 80 per cent of the adult females bring forth young. ($N\sigma^{\prime} = N\varphi$). The numbers of the herd for each year are represented by one column. The diagram shows that up to the year 1903 the curve *a* approximates the theoretical number of breeders and yearlings, but that after that year it falls behind the theoretical increase.

FIG. 5. THE INCREASE OF THE HERD OF ROES (CAPREOLUS CAPREOLUS) IN GATCHINO

The curve *a* drawn on the diagram shows the observed growth of the herd. The constants used in calculating the theoretical distribution are: Initial number of the Herd—$S_0 = 59$, $r = 2$, $j = 2$, the number of the bearing females = 80 per cent of the adult females; unlike Fig. 4 *m* (the value for the mortality rate of the brood) is assumed to correspond to the total numbers of the individuals for each year, and the highest limit of the column for the roes of two years coincides with the curve *a*. The diagram shows the numbers of the age groups of the herd of roes in Gatchino for the summer of every year. The delayed growth as compared with that of Fig. 4 is due to a higher mortality during several years.

period from the birth of the female to the moment of her first parturition must be constant within the limits of each class of vertebrates. We possess for mammals observations of American investigators on the mortality rate among seals (*Callorinchus alascanus*). The seals lose 49 to 50 per cent of their brood during the first year of life. The mortality rate in the brood of the polar fox is also about 50 per cent. Finally I registered in the winter of 1931–32 the number of wild boars in the National Park in the Caucasus and found that the percentage of the surviving brood of the wild boar was 45.5 per cent if we assume, following Dinnik (1910), that the females bear on the average eight young, in reality probably a little less. If on the average there are seven young borne by the female every year, the percentage of survival rises to 50. Thus we see that the mortality rate among the roes coincides very exactly with the theoretical data. The figures obtained are not sufficiently precise and field investigations are needed. I assumed that 50 per cent of the females remained barren every year; however, this number varies in some measure. The mortality rate of the adult roes, which is unknown to us, probably also varied in the course of different years; nevertheless, the coincidence of the curve obtained theoretically with the run of the empirical curve showing the growth of the Gatchino herd is so striking as to allow us to assume with sufficient security that the growth of the herd in reality follows the exponential curve, determined by the constants of reproduction of the species and corrected for the mortality rate of the brood under the age of the first parturition of the female, the mortality rate of the brood being on the whole equal to 50 per cent of the young born every year.

Applying the method of logarithms to the yearly registrations we conclude that the growth of the herd followed the exponential curve and we can also make some additional observations. Plotting the registrations on an arithlog grid we obtain an ascending range of points represented in Figure 6. We see that the points follow with great precision a straight line, this being a proof of the reliability of the statistical data. Examining the disposition of the points more closely we find that the deviation of the points can be explained by fluctuations in the mortality rate of the brood in the course of different

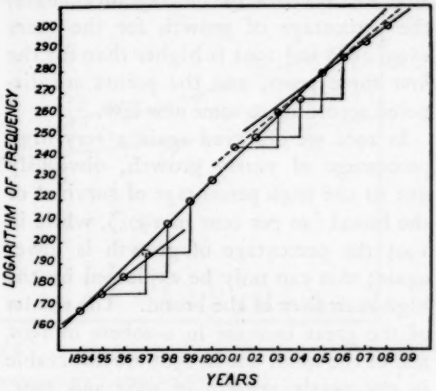

FIG. 6. THE LOGARITHMS OF THE NUMBERS OF THE YEARLY REGISTRATION OF THE ROES (CAPREOLUS CAPREOLUS) IN GATCHINO FROM 1894–1909

The years are marked along the abscissa, the logarithms along the ordinates.

years. The data for the year 1898 being lacking, we had to use the logarithm of the numbers for 1897, adding to it the mean percentage of the growth of the herd for the four nearest years (1895, 1896 and 1898, 1899). The straight line passing through the point of the year 1894 connects the points 1895 and 1896. The longest of the straight lines connects the points 1894, 1899, 1900, 1902, 1903, 1905 and intersects at a certain angle the line connecting the points of the last four years. From this we draw the conclusion that the growth of the herd during these

years was a regular one. This growth is represented by the angle of inclination to the abscissal axis of the straight line connecting the points; it amounts to 21 to 22 per cent a year.

The six roes from the Oural added to the herd in 1895 brought forth their first young in the year 1897; this increased the productiveness of the herd, upsetting the normal proportion of males and females in favor of the females. But we might just as well have assumed a higher percentage of survival of the brood of that year. At any rate the course of the diagram changes; the percentage of growth for the years 1899, 1900 and 1901 is higher than for the first three years, and the points are disposed according to some new law.

In 1902 we observed again a very high percentage of yearly growth, obviously due to the high percentage of survival of the brood (40 per cent in 1901), while in 1903 the percentage of growth is lower again; this can only be explained by the high mortality of the brood. The results of the great increase in numbers in 1902 and of the small one in 1903 are noticeable in the yearly growth in 1904 and 1905, when the females born in 1902 and 1903 bred in their turn; the yearly increase of the next years is more constant. During the last four years from 1906 onwards the increase goes on regularly at a rate approaching that of the growth of the herd for the first five years. The high percentage of survival for the year 1902 was counterbalanced by an increased mortality and by a low rate of growth in 1903 resulting from the high percentage of mortality of the brood. As a result of this the number of the herd attained in 1906 was the same as it would have been if the increase had been going on at the rate of the years 1895–1899.

We have to note one more regularity in the disposition of the points of the diagram. From the year 1898 onwards every point can be connected with the next but one: 1898–1900, 1899–1901, 1900–1902, etc. The population of the roes was registered in Gatchino in November or December of every year; thus the yearlings were registered at the age of seven to eight months, when the period of juvenile mortality was over. The roes mated in August of the following year and the females bore young the following spring after having attained the age of two years; their brood in its turn was registered the following winter at the age of seven to eight months. Thus the connection of each point with the next but one finds its explanation in the age of the first parturition of the female.

The statistical data concerning the population of roes break off in 1909. We do not know what happened after this, but at any rate there were no plagues.

The dynamics of the numbers in the herd of roes shows that the reproduction of a population of vertebrates follows in real life the exponential curve, as determined for each species by the constants of reproduction of the species and by the rate of juvenile mortality. For birds we determined the mortality of the brood as about 90–95 per cent of the total newly hatched brood, for mammals as about 50 per cent of the total new born brood. We certainly cannot expect the precision of these figures to be quite satisfactory and further investigations must be organized with the object of determining the rate of reduction in the numbers of the adults, but in any case the possibility of an analysis such as we have made is in so far interesting as it indicates the possibility of exactly foreseeing the increase of the herd and the construction of the curve of its growth according to constants of reproduction of the species with a correction for juvenile mortality.

We have to draw one more important conclusion from our observations on the rate of reproduction of the roe and of the partridge, this conclusion being confirmed by observations on the growth rate of herds of other animals and birds not mentioned in this paper and also by the relative numbers of groups of fishes (Baranoff, 1917). These observations have a general significance. The yearly reduction in numbers of each older group is fully compensated by the increase in the numbers of the following younger group, capercailyes in Gatchino. The brood was registered every summer, and the adult males every spring on the gathering places for mating. The registration on the gathering places included the adult birds above three years of age, the capercailye attaining its sexual maturity in its third or fourth year; thus only the birds that had survived the period of juvenile mortality were included in the registration.

Comparing the diagram of the registration of the males on their gathering places in spring with that of the females and of

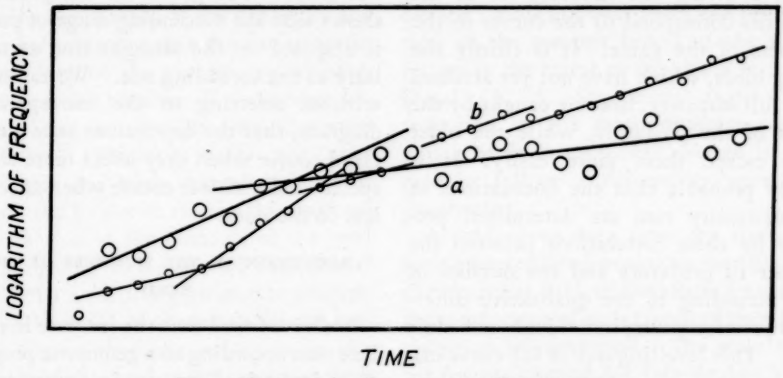

FIG. 7. GROWTH OF A POPULATION OF CAPERCAILYES

a. Logarithms of the registrations of the capercailyes on the nests (the sexually mature female brood of each year). *b*. Logarithms of the capercailyes on the gathering places (the sexually mature individuals). The points in *b* show a smaller deviation from the straight lines than the points in *a*; this can be the case only if the deviations in the mortality rate ot the first and of the second winter stand in an inverse relation to the mortality rate of the spring and of the summer of the first year; the result of this being a more equal growth of the herd of the adults.

consequently the curves of the mortality rate of the land vertebrates and of the fishes correspond to the different age groups forming the herd. Owing to this fact the herd increases in numbers regularly and the current notion that one pair of progenitors is replaced by one pair of descendants proves to be an erroneous one. The regularity of the exponential curve, showing the increase in numbers of the adults in the herd, is caused by the phenomenon which we have observed while studying the rate of reproduction of the the young birds in summer (Fig. 7*a* and *b*) we see that the points representing the males lie closer to the straight line than the points representing the females and the young birds, the latter forming several easily discernible waves. The natural levelling out of the curves of the adult birds can take place only as a result of corresponding fluctuations in the percentage for the figures of early mortality of the brood. The mortality in the years following those when the spring is favorable and the brood numerous will be high and

after an unfavorable spring, the numbers of the brood declining during the summer, the mortality, probably in the course of the following winter, will be less. As a result of this the increase in the number of the adults goes on with greater regularity owing to inverse fluctuations in the intensity of the mortality of the brood at an early and at a later age. The biological aspect of this phenomenon is hardly known, but the fluctuations in the mortality rate probably depend on the changes in the numbers of the predators. The curves showing the shooting off of the predators correspond to the curves in the numbers of the game. It is chiefly the young birds, which have not yet attained their full maturity, that are caught by the claws of the predators, while the older birds escape them more easily. It is highly probable that the fluctuations in the mortality rate are determined precisely by these correlations between the number of predators and the number of prey according to the qualitative differences between young individuals and adult ones. This levelling out of the curve can also be observed in connection with the roe. Thus we come to the following schema: the mortality of the brood per year is about 90 per cent for the birds and 50 per cent for the mammals. The group of the sexually immature surviving individuals and the herd grows regularly during a certain period of time, characteristic for the species. This growth stops abruptly after a plague, affecting not only the brood but the adult individuals as well, and after such a plague a new cycle of reproduction sets in.

Certainly such a simplified cycle represents only a schema of the phenomenon and in reality the process is a much more complicated one. Sometimes the depression is being levelled out; sometimes, given certain constants of reproduction, the depressions are too considerable to be levelled out in the course of one year. The depressions are brought about by different causes and the rate of reduction in the number of the herd may be different. Thus we did not observe any depressions in the given period in the case of the less fertile and comparatively long-lived capercailyes, whereas in the case of the partridge the depression is plainly marked. The reduction in the numbers of the adult individuals, as well as the increase in the numbers, evidently follows the exponential curve. The graph for the partridge shows that the descending range of points is disposed on the straight line as regularly as the ascending one. We can note, without referring to the corresponding diagram, that the depressions take a more rapid course when they affect more fertile species and a slower course when affecting less fertile ones.

REDUCTION IN THE NUMBERS OF THE HERD

We have found that the increase in numbers runs according to a geometric progression determined by species constants of reproduction with a correction for the rate of juvenile mortality for the period j and we have shown, for several examples, that the increase in numbers is abruptly interrupted as a result of periodic plagues caused by abiotic factors or epizootics. A plague resulting from abiotic causes obviously lasts as long as the effect of these causes, for instance, as long as an inundation, as the scarcity of food after a deep snowfall or a dearth; but a plague resulting from an epizootic can last much longer. If the spreading of the disease depends on the density of the population, causing the transmission of the infection, a greater sparseness of the population reduces the possibility of infection, and the disease will gradually slacken. This happens

both in cases of a direct transmission of the infection and in the more complicated cases of infection by helminth parasites with intermediate hosts.

Such infections as pest or anthrax can exterminate an enormous mass of animals in the course of one to two months, but some diseases, and among them evidently the helminth invasions, sometimes spread less rapidly and the rate of reduction can be detected even if the registrations are carried out only once a year. One of the greatest modern mathematicians, Volterra, has developed a theory of the fluctuations in the number of the predators and of the prey, stating that the variations in the numbers of the species preyed upon depend on the number of encounters between these two species. By the word "predators" Volterra means not only quadrupeds and birds, but also agents of disease, and he shows that in this last case the reduction in the numbers of the prey runs according to a negative exponential curve or to a declining geometric progression. The study of the graph for the partridge shows that the reduction in the numbers of the herd as well as its growth actually follows this law, the points of the curve being disposed along a straight line. In reality the process is much more complicated than the case analyzed by Volterra, the reduction in the numbers covering several years and the number of partridges increasing every summer as a result of natural reproduction, whereas Volterra assumes that reproduction is going on uninterruptedly throughout the year.

It is interesting to note that the rate of reduction may be different for different species; for long-lived but not fertile species the period of the reduction in numbers can spread over several years, as is shown by the curve representing the reduction in numbers of the aurochs in the forest of Belovjej in the seventies of the last century.

Thus our observations seem to corroborate the theses of Volterra, although some of his premises rather simplify the question and do not exactly square with the complicated biological relations observed among populations of mammals and birds in nature.

Observations on the rate of reduction in the numbers of the brood in our possession are very scarce, but there are certain indications tending to show that this reduction also follows the law of Volterra. I carried on during two years the registration of the summer brood of the black grouse in the forest of Bashkiria in South Oural (S. A. Severtzoff, 1932). The reduction in the mean numbers of the young birds in each nest proved in this case to follow a descending geometric progression.

According to data from the literature supplemented by observations carried on in the National Park of Bashkiria I assumed the mean value of each clutch of the capercailyes to be eight eggs. The mean number for each brood for July proved to be 4.63, for September 2.82 in 1930 and 2.87 in August, 1931. The data for Gatchino have shown that 90 per cent of the number of birds registered in June and July perish during the winter, thus in our case only 0.463 survived till the age of sexual maturity. Taking the logarithm of these figures, I obtained the diagram (Fig. 8) showing a very regular disposition of the points along the straight line. Further closer observations are certainly needed but in so far as figures are exact we see that the reduction in the numbers of the brood follows a negative exponential curve, the run of which has to be reconstructed according to the diagram; the reduction in the numbers attains its lowest ebb in the spring of the following year, after

this a new cycle of reproduction sets in. A series of observations carried on in the Bashkirian forest shows that the killing off of the birds has to be attributed in the first place to birds and beasts of prey and we see that in this case, as is to be expected according to Volterra, the reduction follows the negative exponential curve, although the biological relation in reality is a different one. Volterra admits an uninterrupted growth of the numbers of the predatory species and a corresponding

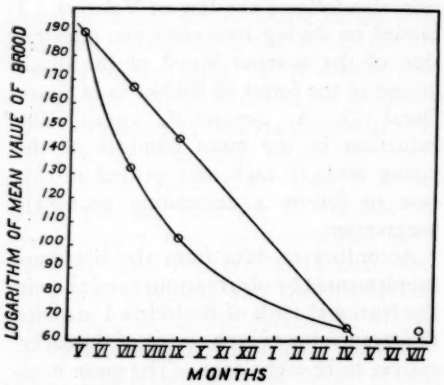

FIG. 8. DIAGRAM OF THE BROOD OF CAPERCAILYES IN THEIR STRUGGLE FOR LIFE

On the abscissa are marked the months from May to July of the following year; on the ordinate, the logarithms of the mean value of the brood for the corresponding months. The curve *b* is a negative exponential curve of the decline of the numbers built up according to the curve *a*.

synchronous decline in the numbers of the prey, but in our case the brood of the predatory birds and animals is brought forth in spring at the same time with the game. During the rest of the year the game is dying off and probably the brood of the predators as well. This process comes to an end before the beginning of a new cycle of reproduction.

In normal years the reduction in the numbers of the individuals that have attained sexual maturity is fully compensated by the young birds, sexually immature, and the following year the group of breeders, both game and predators, will be growing in numbers. This growth goes on until the species of herbivorous animals are exterminated as a result of abiotic factors or of epidemics. The extermination of the prey brings about the dying off of the predatory birds and animals in consequence of the scarcity of food. This picture in real life is much more complicated, the predatory animals being generally euryphagous and not all species of prey perishing simultaneously. But the works of Preeble, Thompson Seton (1909) Elton (1927) and others show that the dying off of the predatory species is connected with plagues among animals forming their chief food. Thus the cycles of growth and of decline in the numbers of the population of herbivorous animals and of the predatory species which feed upon them must coincide more or less.

All the above allows us to build up the following schema of the dynamics of population. The herbivorous animals that have survived a plague bring forth issue in the spring. The dying off of this issue goes on in a declining geometrical progression during the period *j* (for many species this is equal to one year). The surviving brood increases the group of the breeders, the growth of which during a series of years follows the positive exponential curve, as determined by the species constants of reproduction and by the mortality in the first year of life. The length of the period of growth of the herd is determined by the constitution and by the biology of the species as it is precisely those characters of the species worked out in the course of the preceding evolution which determine the amplitude of the fluctuations from the optimum of the conditions of the environment that can be borne by the animal without detriment. The

growth in numbers is interrupted by the next depression in abiotic factors. If such a depression is late in coming and the population goes on increasing, the factors favorable for the development of parasitic agents of disease are gaining in strength together with the growing density, and the growth of the herd is cut off by an epizootic.

Owing to this fact the reproduction of the herd as well as the dying off of the yearly issue follows a negative exponential curve; the mortality affecting the adult animals as well, the number of the herd reaches its lowest ebb; after this a new growth of the herd sets in. The curve representing the dynamics of the carnivorous species preying upon the herbivorous ones runs parallel to that of the herbivorous species and the cycle of growth of the herd may be of the same length, but in some cases when the predatory animals can migrate in time into an area where the plague is not yet developed, or when they can be content with a substitute food, there may be deviations from the rule.

BIOLOGICAL CAPACITY OF THE HABITAT

Thus far we have spoken only of the processes of the increase and of the decline in the numbers of the herd in time, without discussing the important problem of the biological capacity of the habitat occupied by the population. But the numbers of the population of different species in the same locality are different, and therefore the absolute number of the individuals needed for attaining the highest density for any species will be a different one for each species.

The increase of the herd goes on in a geometrical progression, as determined by species constants of reproduction; it is so intense that all species, even the least fertile ones, fill in the area suitable for their habitation in a very short period of time. Travellers investigating countries hardly changed by the interference of man describe herds consisting of millions of animals of slow reproduction, such as the bison in the prairies of America, and enormous flocks of seals. Darwin wrote that the albatross, the reproduction of which is very slow, is perhaps the most numerous bird on earth; we can also mention the immense flocks of the migratory dove and lastly the enormous number of ungulates in Africa in the beginning of the last century. All these examples show that the absolute number of any species may be very great in spite of its relatively low fertility.

CORRELATION BETWEEN DURATION OF LIFE AND FERTILITY

In my paper of 1930 I proceeded from the idea that the duration of life of each animal determines the limiting number of the generations which can exist simultaneously in the habitat of the species. Those individuals that have survived the period of juvenile mortality forming a stable population, the duration of life of the individuals of each species must correspond to the period between two consecutive plagues, this period being characteristic for each species. Proceeding from this idea I studied the relation between the duration of life and the fertility of mammals. I have calculated the correlation between the index of the species fertility q and the species duration of life T. I reasoned as follows: Let the number of pairs of individual breeders that have survived the plague be S_0, the number of the individuals to the end of the cycle of reproduction t will be S_t; then we can write

$$S_t = S_0 q^t .$$

Consequently S_t is directly proportional to S_0 and q^t. After putting this expression

in logarithmic terms and transferring log q and log S_0 to the left side we write:

$$\frac{\log S_t - \log S_0}{\log q} = t,$$

or if

$$\log S_t - \log S_0 = \log \frac{S_t}{S_0} = \log W,$$

then

$$\frac{\log W}{\log q} = t.$$

Log W represents the intensity of the plague, log q the rate of growth of the population, t is the time interval in which S_0 grows into S_t. From the equation

$$\frac{\log W}{\log q} = t,$$

log W is directly proportional to t and inversely proportional to log q. If log q is constant and t and W variable, we can say: the longer is t, the greater is the density attained by the population and the stronger is the plague

$$(S_t/S_0 = W).$$

If t is a constant (and we tried in our work to show that the period of growth of the herd must be a very constant one) then the left side of the equation

$$\frac{\log W}{\log q} = t$$

must also be constant; this is possible if log W and log q change in inverse proportion. During the period between the two great plagues which bring S_t to S_0 there occur depressions of a smaller intensity, which upset the rate of increase of the herd and put off the time when the number S_t can be attained.

While examining the rate of reproduction of the roe and of the capercailyes we have seen that the high mortality setting in from time to time is accompanied by the corresponding increase of the fertility of the herd. This increase is obtained either indirectly by the reduced mortality rate among the brood or else directly by the increase in number of the young brought forth by the females and also by a lower percentage of barrenness of the females, in other words by the increase in the numbers of the issue brought forth by the herd as a whole. The last case is specially important for species which do not bear every year, but after longer intervals of time, as the aurochs (*Bison bonasus*).

We do not know whether the violence of the plagues has undergone any variations in the course of evolution or not, but there seem to be some indications pointing to the reduction of the violence of the fluctuations in the course of evolution; the decline in the numbers of fertile rodents, hares, and lemmings, was evidently much more considerable than the 60 per cent found in Gatchino for the herd of partridges, but the data available are not sufficiently precise.

Assuming the duration of life of the individuals to correspond to the frequency of the plagues, it is possible to show that the fertility is reduced in accordance with the growing longevity during the evolution of species. For 78 species of mammals the coefficient of correlation between the duration of life of the species T and the logarithm of the index of the species fertility q is -0.899 ± 0.0238, but it is obvious that the species evolved divergently and that in the course of evolution some of them acquired a greater longevity, and others a smaller one, their fertility varying according to the equation

$$\frac{\log W}{\log q} = T.$$

LAWS OF VOLTERRA

We have repeatedly mentioned in this paper the works of Volterra, pointing out that his fundamental conclusions are corroborated by observations on the rate of reproduction of the vertebrates and it is proper to cite in this place his essential theses (Volterra, V., 1930).

1. The law of the periodic cycle: The fluctuations in the numbers of both species are periodic, the period being determined by the rate of growth and of reduction in the numbers of the population and by the original ratio of the numbers.

2. The law of conservation of the mean number: The mean number of individuals of both species remains constant; as such it is determined by the initial number as long as the rates of growth and of decline in numbers (birth-rate) remain stable and as long as the coefficients of defense and aggression remain invariable. This means that both species fluctuate about a state of statistical equilibrium which is never attained, the mean number for each species being assumed to be a constant one.

3. The law or rule of the disturbance of the mean value: When there is an attempt to kill off individuals of both species in equal proportions, the relative numbers of the species preyed upon increase and those of the predatory species will be reduced. The diminution of killing of the species preyed upon also increases the number of the predatory species.

The following laws can be applied to cases when the fluctuations are not great: 1) small fluctuations are isochronous, which means that the period of these fluctuations does not depend in a noticeable way on the initial number of the individuals and is solely determined by the correlation between the coefficients of defense and of aggression; 2) the period of the fluctuations is proportional to the geometric mean of the periods of time during which the first species doubles its numbers and the second one is reduced to half its numbers; 3) in the case of equal fluctuation—the population being reduced by an equal number of individuals during equal periods of time—the killing off of the individuals of the carnivorous species accelerates the fluctuations, while the reduction in the numbers of the species preyed upon delays it.

Our observations show that the growth of the herd follows the exponential curve determined for each species by its constants of reproduction. The reduction of the herd in so far as it depends on biological agencies also follows the negative exponential curve, as was admitted by Volterra, but the general picture of the fluctuations, in the numbers of vertebrates at least, is different from the picture suggested by Volterra. The curves of growth and of reduction of the herd are not symmetrical; the curve of growth is a more slanting one, that of reduction a more rapidly descending one.

The quadruped beasts of prey do not reduce the number of the herbivorous species periodically as is supposed by Volterra. The numbers of the carnivores increase with the increase in the population of the herbivores and they die off simultaneously with the latter. Volterra's theory of uninterrupted fluctuations is probably right in connection with epidemic diseases caused by parasites, when the infection is a function of the number of the herd and of the frequency of the encounters between the infected and the uninfected individuals.

We can evidently point out another very interesting circumstance which, however, has still to be verified and further investigated. According to Volterra, if the predatory species and the species preyed upon are killed off in an equal measure by any third cause, as for instance

by man, the numbers of the predatory species fall lower than the numbers of the species preyed upon. This is quite natural biologically, the number of the predatory species being reduced not only in consequence of their direct extermination but also in consequence of the scarcity of food resulting from the killing off of the herbivorous species.

The correlation table between the duration of life and the fertility of mammals (S. A. Severtzoff, 1930) shows that, the duration of life being equal, the predatory species possess a greater fertility than the species of herbivorous animals they feed upon. At the same time we know that the relative numbers of the predators are always less than the numbers of the herbivores. This contradiction between the coefficient of potential fertility and the relatively small numbers of the carnivorous species makes us assume that the mortality rates of the brood and of the adults are higher among the latter species than the same rates among the herbivores, the predators perishing not only from causes bringing about their own extermination, but also from causes exterminating the species they feed upon. The smaller resistance of the predacious species against agencies of the environment is compensated by a greater fertility. We can see in this fact a biological phenomenon worked out in the course of evolution and levelling out the effects of the law deduced by Volterra on the basis of a theoretical analysis of the problem.

SUMMARY AND DISCUSSION

1. The numbers of each species of animal are not constant but increase yearly as a result of natural reproduction on an exponential curve determined by the inherited characters of the species with a correction for the mortality of the yearly brood and of the adults.

2. The mortality rate of the brood is about 90 per cent for the birds and 50 per cent for the mammals, this reduction covering on the whole the yearly reduction in the numbers of the adult breeders.

3. The reduction in the numbers of the brood follows the negative exponential curve.

4. The increase in the numbers of animals of any species is cut short by plagues, caused by abiotic factors after certain periods of time characteristic for each species and determined by the capacity of the species to withstand extreme deviations of external conditions from the optimum; after these plagues the reproduction of the species goes on according to the former law.

5. In order to secure the survival of a number of individuals sufficient for the continuation of the race, the species have to attain their highest possible numbers in the course of the period favorable for reproduction.

6. If the density of the population is not decreased in time by abiotic factors, it will be decreased by an epidemic disease, the higher density of the population being favorable to the spreading of the epidemic.

7. The predatory species only delay the increase in the numbers of the herbivorous species, exterminating the greater part of the yearly brood, but they do not interrupt the growth. Diseases caused by parasitic agents reduce the numbers of the vertebrates; in this case the reduction follows the negative exponential curve and lasts till the numbers of the herd have attained a certain minimum.

From this picture we may derive some conclusions about the evolution of fertility. The question being a very complicated one, we intend to devote a special article to its analysis and we shall confine ourselves here to general conclusions.

The constants of reproduction of the

species as well as the mortality rate among their brood and among the adults vary in the course of evolution. Comparing different species, as is done in comparative morphology, we can imagine the evolution of the biology of the species. There is a different curve of the mortality rate corresponding to each given moment of the existence of the species and also a different cycle of growth and of reduction in the numbers of the herd, the reduction in numbers being compensated by the fertility of the species and corresponding to the longevity of the individual as characteristic of the species.

This balance is only an apparent one, and the species are undergoing unceasing variations as a result of the struggle for life; we shall be able to show this on the existing fauna when we have acquired the means of comparing more minutely and with greater precision the fertility and the longevity of kindred species and perhaps of different colonies of the same species. The adaptation of each species to the condition of the environment is increasing in the course of evolution. Since each degree of growing adaptation increases the survival of the individuals, they acquire a greater longevity. The number of individuals existing in the herd at any moment is growing in this case as a result of the birth of young individuals and also of a greater duration of life of the adults. There are different factors entering into this growing adaptation. For instance: 1) increased resistance of the individual to abiotic factors resulting in the lengthening of the period between two plagues caused by abiotic factors; 2) improved equipment of the prey for defense resulting in a lower percentage of killing by predatory species; 3) improved equipment for aggression of the predatory birds and beasts and their greater ability to procure food, bringing about a lower percentage of survival of the corresponding species preyed upon and this in its turn resulting in a higher mortality of the predators, etc. On the whole a higher adaptability must prolong the duration of life of the individual.

But the cycle of growth in the numbers of the population will hardly be lengthened and this newly acquired duration of life hardly takes place as both these phenomena reinforce the conditions of the development of infectious diseases which in their turn interrupt the growth of the population as soon as it attains a certain limit; consequently the infectious diseases prolong the cycle of growth of the herd and only the populations with a reduced fertility will be able to prolong the biological duration of life of the individual beyond these limits.

A reduced fertility of the population is acquired in some cases owing to a higher age of the first parturition (j) and to a longer period between two consecutive births (p). But the reduction in the numbers of the brood must be the predominating factor in the cases when the species are breeding at the age of one year. Thus the agents of epidemics are causes of the selection of the least fertile populations, when the same result is not attained by the evolution of individual development. Finally it is necessary to point out that the mortality rate of the brood must increase as a result of a greater competition with more numerous and fully developed adult individuals. All these causes must act as factors delaying the progressive evolution of the species.

Further we can imagine the process of the shortening of longevity in the course of evolution as a result of an increasing frequency of plagues from abiotic factors or as a result of a higher coefficient of predacity of carnivorous animals.

The growing frequency of climatic de-

pressions, as at the approach of the glacial period, can be survived only by fertile species or by species with an increasing fertility which succeed in restoring their former level in periods of time shorter than formerly. I am inclined to think for many reasons that this is rarely the case.

Of greater significance is the second case: Volterra's higher coefficient of predacity—an increasing extermination of herbivorous animals by predators; the phytophagous must either acquire a greater fertility or they must disappear from the face of the earth. The following arguments seem to be conclusive that such a secondary increase of fertility due to secondary causes took place among the mammals: the reduction in the numbers of the young borne by the female corresponds to the reduction of the milk-glands. We find that the milk-glands of primitive mammals were very numerous (the Centetes had up to 24 pairs, while the fertile rodents have not more than 6–8 pairs); consequently a process of reduction of the brood and of prolongation of longevity has taken place among their ancestors. The fertility of mice and hares is very great as they breed several times a season and some of them attain sexual maturity so early that they breed in their turn during the same summer when they were born. This phenomenon is a secondary one and it corresponds to an increase of fertility due to secondary causes and compensating the growing extermination by predacious animals and a lower duration of life of the individual. According to this the reproduction of the rodents is so rapid that their duration of life does not coincide with the frequency of the climatic depressions and that these species generally perish as a result of periodic epizootics. Thus the most characteristic factors in the biology of the rodents, of the ungulates and of the predatory species find their explanation in the evolution of the ecology of reproduction.

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MOVEMENT IN THE CYANOPHYCEAE

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THE autonomic movements of filamentous Cyanophyceae have attracted the attention of numerous investigators from the time of Adanson (1767), and have evoked a considerable literature describing the visible character of these movements and attempting to explain their as yet cryptic cause. Among the early algological records are the observations of Vaucher (1803) dealing with movement in the young filaments of *Nostoc* and the writings of Schrank (1813) and of Borys de St. Vincent (1827) describing the motility of *Oscillatoria*. The latter author, after presenting a vivid and somewhat amusing description of the behavior of "Oscillaire" filaments, was obliged to conclude with the remarks: "Nous avons renoncé à trouver leur mode de reproduction, et surtout à expliquer le mécanisme et les raisons de leurs mouvements." Exactly one century later one may read in West and Fritsch's (1927) excellent treatise on the algae that "although these movements have been much studied, especially those of the Oscillatoriaceae, no convincing explanation as to the mechanism has yet been offered."

The early workers were concerned with descriptive morphology and taxonomy rather than with the acquisition of knowledge by experimental methods. It should be pointed out, furthermore, that in many instances problems such as this are not solved until a considerable background of general information has accumulated and suitable methods for experimentation have been devised. The problem of movement in the blue green algae, however interesting to botanists, was not approached experimentally until comparatively recent years.

The motility of the Cyanophyceae is of itself interesting, and the more so because of the striking similarity between this particular type of movement and that exhibited elsewhere in nature, *i.e.*, the locomotion of thiobacteria, diatoms, and desmids among plants, and the movements of amoebae, gregarines, phagocytes, etc. in the animal kingdom. All these relatively simple structures exhibit no permanent organs specialized in relation to locomotion; it is quite possible that no great dissimilarity exists in the fundamental mechanisms which activate them all, though the controlling influences may be different in specific instances. It is our purpose here to bring together the results from the scattered literature pertaining to this subject, and to consider the problem of the mechanism of the movement.

NATURE OF THE MOVEMENT

Several different aspects of movement are apparent in the filamentous Cyanophyceae, *i.e.*, linear translation, axial rotation, and oscillation (*cf.* West, 1916). The translatory type of movement commonly consists of a slow gliding of the filament over a solid substratum in a straight or spiral line, the direction of which may be subjected to sudden and repeated reversal. According to Borzi (1886) the hormogones

of *Lyngbya*, *Plectonema*, *Nostoc*, *Rivularia*, *Scytonema*, and *Stigonema* emerge from their sheaths and exhibit periodic movement in a straight line for short periods of time; but the filaments of *Microcoleus*, *Oscillatoria* and *Spirulina* are characterized by persistent movement in a spiral path. Characteristic linear progression of either the hormogones or the ordinary filaments of these and other genera (*Anabaena*, *Cylindrospermum*, *Gloeotrichia*, *Isocystis*, *Phormidium*, etc.) have been described by many persons (Corti, 1774; Meyen, 1839; De Bary, 1863; Schwendener, 1894; Brand, 1903; Phillips, 1904; etc.).

This typical linear progression is in some instances (especially in the Oscillatoriaceae) accompanied by continuous rotation on the axis of the filament. The direction of rotation, to the right or left, is held to be constant for a given species of *Oscillatoria* (Schmid, 1921) and has indeed been employed in the description of species in Geitler's taxonomic treatise on the group (1925). The manner of rotation outwardly suggests the characteristic rotatory powers of flagellates, ciliates, rotifers, etc. and may be determined by the definite morphology of the organisms. Through failure of all parts of a filament to cooperate, torsion may result in the twining of the *Oscillatoria* filaments about various small objects or each other (Fechner, 1915; Schmid, 1918). In *Spirulina* there is a well-marked rotation about the axis of the spirally twisted trichome during its screw-like progression through the water (West and Fritsch, 1927). Certain species of *Oscillatoria* exhibit a bending of the apical cells which is evident during rotation of the filament. Observations seem to indicate that rotation probably does not occur in the heterocystic members of the group (Borzi, 1886; Harder, 1918; Castle, 1926; etc.) and probably not in all species of *Oscillatoria* (Crozier and Federighi, 1924). It is probable that the spiral course characteristic of many members of the Oscillatoriaceae while moving freely in suspension may be considerably modified under conditions where the organisms are caused to adhere to a solid substratum.

The third type of movement has to do with the bending and swinging of the end of a filament in a conical path. The swinging of a free end frequently occurs while the other end is held in a colonial mass of the organisms, but may also be found in unimpeded, creeping filaments. Also a bending of the extreme apical portion is commonly exhibited. When the motion is artificially restricted to a narrow plane, as is usually the case in a microscopic preparation, there is presented the appearance of slow pendulatory oscillation which has doubtless given rise to the generic name, *Oscillatoria*. These swinging movements have been related to unequal stretching of the cell membranes on opposite sides of the filament correlated with a simultaneous rotation of the trichome (Schmid, 1918).

Autonomous movements have upon several occasions been ascribed to single zoospore-like cells of the blue green algae (Borzi, 1880; Davis, 1894; Zukal, 1894), but such reports have been few and are perhaps of somewhat dubious authenticity. Recently the detachment of motile blue green cells from the apex of *Oscillatoria* and their swimming about in zoospore-like fashion has been reported by Spearing (1932). The correct interpretation of these reports is as yet by no means clear.

Of these various types of movement, that of longitudinal progression is probably best suited for experimental analysis, since it has been shown to be very steady under constant conditions (Crozier and Federighi, 1924). The rate of movement

under favorable conditions varies in different species up to a maximum of about 2 to 5 microns per second at ordinary room temperature (*cf.* Gicklhorn, 1921; Crozier and Federighi, 1924; Castle, 1926; etc.). Unlike the simple linear progression of *Nostoc*, *Anabaena*, etc., the trail of an *Oscillatoria* filament appears under close examination to assume the form of a curved path. According to Schmid (1921) this path is the result of two vector components, one associated with the longitudinal velocity and the other with the rate of axial rotation at right angles to the filament.

The situation may be elucidated by the diagram in Figure 1 showing a camera-lucida sketch of the trail made by a filament of *Oscillatoria sancta* creeping on the surface of nutrient agar. The alga was started at the point *X*, with the filament axis perpendicular to the rays of incident light coming from the right. In this instance the direction of axial rotation was to the right, hence the filament progressed in a curved course until the position *Y* was attained. At this spot reversal occurred and the filament, always turning to the right, moved again nearer the source of illumination by a curved route. The

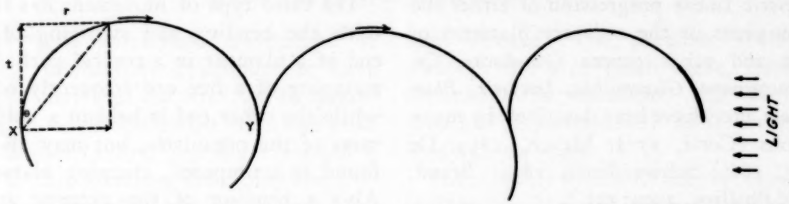

FIG. 1. THE TRAIL OF OSCILLATORIA SANCTA CREEPING ON 1 PER CENT AGAR TOWARD THE LIGHT
The angle θ denotes the deviation from a straight line resulting from the combination of longitudinal movement (t) and axial rotation (r).

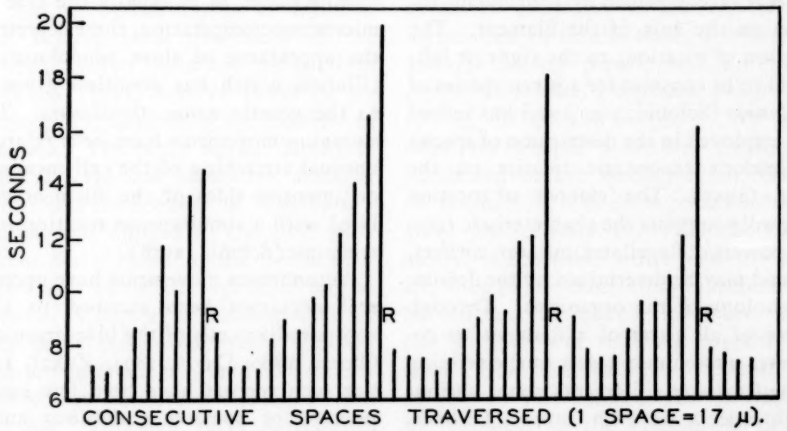

FIG. 2. VARIATION IN VELOCITY OF TRANSLATORY MOVEMENT ASSOCIATED WITH REVERSAL OF DIRECTION IN OSCILLATORIA FORMOSA

The speed gradually decreases prior to reversal and suddenly increases immediately afterward in rhythmic fashion. If a reversal be denoted by *R*, the succeeding ocular spaces (17μ each) are traversed in 8.6, 7.2, 7.2, ... 16.5, 19.9 seconds. Following this gradual decrease in speed, a sudden increased velocity reoccurs upon reversal (*R*); etc.

shape of the curve may be stated simply to be dependent upon the component of linear translation, t, and that of revolution, r, about the filament axis. The angle θ may be taken to represent the deviation from a straight line, and tan $\theta = r/t$ or $\pi\ d/t$ (d = diameter of the filament). This type of observation might very well be employed in the further investigation of the effect of controlled variables upon orientation and reversal of these organisms.

STRUCTURE OF THE ORGANISMS

It is beyond the purpose of this paper to deal with details of morphological and cytological structure in a comprehensive manner, but a few essential facts will be pointed out in order to clarify the possible relationship between structure and certain physiological processes in these organisms.

The question of cell structure in the Cyanophyceae has long been a subject of controversy, but the general situation is fairly well established for those members of the group with which we are here concerned. The protoplast is described as consisting of three regions: a central mass of not very highly organized chromatin material, a peripheral portion which contains the characteristic pigments, and the outer plasma membrane in direct contact with the cell wall (*cf.* Olive, 1904; Gardner, 1906; Guillermond, 1906; Brown, 1911; *cf.* Sharp, 1926; etc.). Cell division is accomplished essentially by amitosis, which results in the quantitative separation of the chromatic material (*cf.* Smith, 1933), and the formation of a ring-like wall which grows inward from the lateral wall. The pigments chlorophyll, carotin, phycoerythrin, and phycocyanin are distributed throughout the peripheral undifferentiated chromatophore mass in diverse proportions (Boresch, 1921; Wille, 1922) dependent upon the wave-length and the intensity of the illumination (Gaidukov, 1903; Harder, 1923; Sargent, 1934) and the nutrient conditions (Magnus and Schindler, 1912; Schindler, 1913; Boresch, 1920, 1921).

Since the Cyanophyceae are not characterized by definitely differentiated chromatophores, such as hold the pigments in most other autotrophic plants, these algae appear to afford certain distinct advantages as material for the study of photosynthesis. It is suggested that the substances concerned in the reactions of photosynthesis are in this instance relatively free to diffuse throughout the pigmented region which is uncomplicated by differentiated structure. However, there exists the problem of obtaining pure cultures of the algae, which to date has not been solved satisfactorily.

The first evident products of photosynthesis are sugars and glycogen, and according to Baumgärtel (1920) these are immediately converted into glycoproteins (cyanophycin granules of Gardner, 1906), which accumulates as stored reserve food in the peripheral cytoplasm. Starch never occurs, but small oil droplets are frequent inclusions, as also are the much disputed "pseudo-vacuoles" in many genera (Brand, 1905; VanGoor, 1925). The blue green algae are generally devoid of true vacuoles and for this reason are able to endure long periods of drought (West and Fritsch, 1927).

Enzyme activity has been studied in various green algae (Hampton and Baas-Becking, 1920; Sjöberg, 1920; Burge and Burge, 1924; etc.), but little is known about the enzymes of Cyanophyceae. Lavela (1925) found that *Phormidium laminosum* growing in springs at 74°C. produces lipase and a glycogen-splitting enzyme, but neither diastase, invertase, nor casein-splitting enzymes. According to Schmid (1921), *Oscillatoria* produces

an agar-dissolving ferment. An indirect approach to the study of catalytic processes in the activity of *Oscillatoria* has been indicated by Crozier and Stier (1926) in a discussion of the meaning of their thermal increment data. No further data upon the enzymes of blue green algae have been found.

The cell wall in the filamentous Cyanophyceae is regarded as consisting of two investments, an inner somewhat modified plasmatic membrane, and an outer mucilaginous envelope of firmer consistency (Lemmermann, 1910) forming a cylindrical sheath which is continuous (as in *Oscillatoria*) or interrupted between the cells (as in *Anabaena*; Fritsch, 1905). Geitler (1925) holds that all cyanophyceous cell walls consist of pectins, but contain neither chitin nor cellulose. Mameli (1920) has claimed the absence of chitin (*cf.* also Wester, 1909) and affirmed the presence of cellulose and pectins. Ullrich (1929) has since demonstrated hemi-cellulose together with pectins in the cell walls of *Oscillatoria*.

There is no complete agreement concerning the wall structure, some having claimed it to be net-like (Correns, 1897; Kolkwitz, 1897), others finding it homogeneous (Krenner, 1925; Ullrich, 1926). Many investigators have reported regularly arranged pores in the longitudinal walls of *Oscillatoria* (Kolkwitz, 1897; Phillips, 1904; Schmid, 1921). By using KI and H_2SO_4, Schmid (1921) was able to discover pores in the longitudinal as well as in the cross walls of *O. Jenensis*. However, Ullrich (1926) was unable to discern any pores by employing KI and KOH. That the adjacent cells of the Hormogoniales are connected by plasmodesma extending through pores in the transverse walls (thus unifying the entire filament) has been held by Wille (1883), Borzi (1886), Phillips (1904) and others. West and Fritsch (1927) suggest that the pores of *Stigonema* can be rendered conspicuous by desiccation and subsequent resoaking in water. Phillips (1904) recommends immersing the material in palladious chloride for a few days to increase the size of the pores. From the literature it is apparent that the visible details of structure depend upon the methods employed in fixation and staining of the material.

One property of the cell walls which appears to be intimately concerned with the movements of these organisms should be emphasized, *i.e.*, their remarkable elasticity. Measurements of the range of elasticity have been made by the plasmolytic method (Brand, 1903), and also stereoscopically under normal culture conditions (Ullrich, 1926, 1929). Species of small diameter have been found capable of the largest percentage of stretching (*cf.* Hansgirg, 1883; Schmid, 1918).

The secondary cell sheaths not in direct contact with the protoplast are held to be developed either by apposition of new inner layers of mucus (Correns, 1897), by intussusception (Geitler, 1925 *a*), or commonly by the extrusion of carbohydrate substances through pores in the cell membrane (Kolkwitz, 1897; Schmid, 1921). Fechner (1915) found that by staining with safranin the uneven appearance of the mucilaginous surface in *Oscillatoria* could be made to reveal crossing systems of material arranged at an angle of 35° to the axis of the filament. That secretion takes place in the apical cells only and that the slime gradually moves toward the middle (Fechner, 1915; Gicklhorn, 1921) is denied by Schmid (1921), who claims that secretion occurs along all portions of the filament.

The conditions governing the rate of sheath-formation (which a host of persons have invoked to explain motility) have

to date not received critical attention. Presumably the factors which influence the elaboration of food materials in the plant and the factors which regulate the turgor pressure of the cell and the permeability of its membrane are involved in producing the extruded mucus substances.

The chemical nature of the envelope, which may be extremely thin (*Oscillatoria*) or very thick (*Lyngbya*), varies according to the species. Among the earlier investigators, Gomont (1888) found that

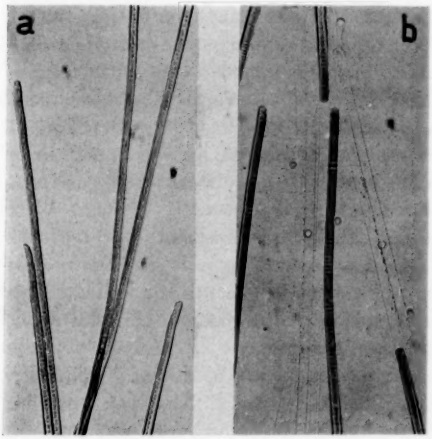

FIG. 3. ILLUSTRATION OF THE VARIABLE NATURE OF THE GELATINOUS SHEATH

(a) No sheath present in *Oscillatoria formosa*. (b) In old cultures the same species is provided with a definite sheath.

although the cell *membrane propre* was insoluble in acids, the sheath was readily soluble and consisted of layers. In an investigation of many genera, Lemaire (1901) concluded that the filamentous Cyanophyceae exhibit three types of sheaths: (1) simple sheaths composed of pectin (*Anabaena*, *Cylindrospermum*, *Gloeotrichia*, *Nodularia*, *Nostoc*), (2) complex type consisting of acid pectins and basic "schizophycose" (*Lyngbya*, *Phormidium*, *Scytonema*, *Stigonema*), (3) mixtures of cellulose and "schizophycose" (*Desmonema*, *Diplocolon*, *Scytonema*, *Tolypothrix*).

Among the later inquiries into the nature of the cyanophyceous sheath was that of Klein (1915), who denied that chitin is a constituent as had been reported earlier (*cf.* Hegler, 1901; Kohl, 1903). Cellulose was demonstrated in the heterocysts and sheaths of *Dicothrix*, *Rivularia*, *Schizothrix*, *Scytonema*, and *Tolypothrix*, but was not found in the sheath of *Lyngbya*. In the sheaths of many genera, pectin was found to be a common constituent, and in *Nostoc* pentosans were found. The thin sheath of *Oscillatoria* (visible in ink suspensions) has not been studied so extensively. Krenner (1925) claimed that hemicellulose, not pectin, forms the isotropic sheath of *O. limosa* (disagreeing with Kohl, 1903, and Fechner, 1915); Ullrich (1929) has reported that (as an artifact) the pectin-hemicellulose sheaths of *Oscillatoria* sp. may be doubly refractive when under pressure.

The sheath (its size, color, etc.) has long been regarded as an important morphological character worthy of the attention of descriptive taxonomists. On the authority of Gomont (1888), the presence of a sheath is the only character which separates the genus *Lyngbya* from the genus *Oscillatoria*. It appears doubtful whether this distinction can in all cases be maintained, based as it is upon a variable character whose quantity at any time must in large measure be dependent upon the factors of the environment. The thickness of the sheath will depend upon the amount of new material which can be excreted by the protoplast upon the internal surface of the older layers of mucus. If a filament be non-motile or subjected to frequent reversal, more mucus can be accumulated about it than in the case of a filament proceeding without reversal at a relatively rapid rate over a long distance

and continually leaving its mucus behind on the substratum (*cf.* Phillips, 1904). Two algae, one answering the description for *O. formosa* and the other for *O. sancta*, were observed recently to have well-developed sheaths in old cultures. When transferred to fresh solutions favorable for the exhibition of translatory movement, the trichomes always glided out leaving the old sheaths behind (*cf.* also Phillips, 1904; Coupin, 1922). This phenomenon is supposed to represent the so-called reproduction by hormogone formation, but is apparently not related to the length of the filaments. It would appear that thickness of the sheath in at least some of the Hormogoniales is a variable quantity which depends as much upon the external environmental factors which influence the synthesis of carbohydrate materials and movement of the organisms as upon internal hereditary factors.

Summarily, it may be said that the Cyanophyceae, characterized by relatively simple cell- and body-structure, very well illustrate "the conception of cell structure which implies differentiated regions of a colloidal system in which special processes have become localized and tend to remain fixed" (Harper, 1919).

THE MECHANISM OF MOVEMENT

Of all the various theories which have been proposed to explain the mechanism of movement in the Cyanophyceae, probably the most popular is that involving the mucus secretions which form the sheath. The secretory mechanism (*cf.* Verworn, 1899) has long been held to be the cause of motility, not only in the blue green algae (Engelmann, 1879; Correns, 1897; Fechner, 1915; Gicklhorn, 1921; etc.) but also in the desmids (Klebs, 1886; Aderhold, 1888; Schröder, 1902) and diatoms (Bütschli, 1892; Lauterborn, 1894, 1896) as well. One point of view would propose that the actual streaming of the outer mucus (plasmic strands), as indicated by the movement of adhering foreign particles, serves to propel the cyanophyceous filament (Siebold, 1849, Schultze, 1865; *cf.* Fechner, 1915) in much the same manner as in the case of diatom frustules (Müller, 1893, 1897; Lauterborn, 1896; Palmer, 1910) and perhaps some amoebae. Engelmann (1879) went so far as to identify the outer mucous material of *Oscillatoria* as a modified plasma membrane, and Schultz had previously held the idea of pseudopodial action in the case of diatom movements. Fechner's (1915) contention that only the apical parts of a filament contribute to movement by secretion of slime was disproved by the experiments of Schmid (1923) with severed portions, in which all parts of a filament were found capable of movement.

In this connection it is significant that streaming inside the cell, as indicated by the motion of cytoplasmic granules under the ultra-microscope, occurs only while the algal filament is in motion (Gaidukov, 1910; Schmid, 1918). That the puzzling movements of diatom frustules may be related definitely to protoplasmic movements has been suggested recently by Dangeard (1931). The inhibitory effect of ultra-violet light upon movement in *Oscillatoria* was attributed to an effect upon the *kontractile Substanz* of the protoplasm by Fuchs (1907). In view of what is known about protoplasmic streaming in such plants as *Elodea*, *Nitella*, etc., it appears not unlikely that the movements of the Cyanophyceae may be related in a definite manner to the activity of the protoplasts, perhaps through the excretion of streaming mucous material.

A somewhat different viewpoint involves the radial swelling of the anisotropic mucus to form a narrow angle which

squeezes the filament forward and away from the smaller end of the sheath (Fechner, 1915; Harder, 1918). This theory might possibly be applied to the cylindrical Oscillatoriaceae, but it would seem difficult to apply to those heterocystic forms in which the mucous sheath is interrupted between the cells (*cf.* Fritsch, 1905). The anisotropic character of the sheath has been denied by several later workers and the swelling theory stoutly denied by Schmid (1918).

Prell (1921) advanced the hypothesis that movement might be caused by the flowing pressure of gelatinous strands extruded through the numerous spirally arranged pores along the entire length of the filament. These strands of jelly presumably correspond with the position of the pores and are originally separate; final agglutination by swelling results in the characteristic sheath formation. The direction of rotation in screw-like fashion is held to be morphologically fixed by the spiral arrangement of two crossing series of pores; reversal is explained as a response to some external stimulus which checks secretion and causes contraction of the filament. When secretion is resumed, the strands of jelly have a different purchase with respect to the substratum and the filament is caused to move in the opposite direction. This ingenious hypothesis was built upon the work of preceding authors (Fechner, 1915; Schmid, 1918) and has considerable evidence in its favor. In the desmids and the recently described *Chroothece mobilis* (Pascher and Petrova, 1931) the pores are sufficiently large so as to extrude quite easily discernible mucous strands which are believed to cause movement; in the Cyanophyceae, however, the optical evidence in support of Prell's hypothesis is not wholly satisfactory. The observations of Phillips (1904), who erroneously concluded from his data that the extruded protoplasmic strands function as cilia, seem to lend evidence in favor of a secretory mechanism like that proposed by Prell's hypothesis.

The various theories of propulsion by mucilaginous secretions appear less easily applied to the movement of filaments not in direct contact with a solid substratum. Several early workers (Cohn, 1867; Hansgirg, 1883) believed that longitudinal progression took place only while the organisms were in contact with a substratum, but free swimming has since been observed in *Cylindrospermum*, *Oscillatoria*, *Spirulina*, etc. (Nägeli, Pfitzer cited in Vines, 1886; Kolkwitz, 1897; Phillips, 1904; West and Fritsch, 1927). Kolkwitz (1897) noted also the creeping locomotion of *Oscillatoria* on the surface of the water. The author has observed that movement during free suspension in culture solutions, though infrequently encountered, is more rapid than while in contact with a glass surface. To quote Vines (1886): "The creeping movements are suggestive of pseudopodial action but the swimming power would appear to lend support to an osmotic theory."

The osmotic theory of movement has had many proponents in the past, *e.g.* Borscow, Dippel, Hansgirg, Mereschowsky, Nägeli, etc. (*cf.* Vines, 1886). Zukal (1880) working with *Spirulina* thought that unequal growth on different sides of the filament would cause distortion of the hydrostatic pressure and hence effect movement. The theory postulated by Hansgirg (1883, 1887) would attribute movement to diosmotic processes resulting from a turgor gradient along the entire filament. When turgor is greater in the cells at one end than at the other, movement continues steadily, but due to an external stimulus (*e.g.* friction of the foundation) the turgor pressure gradient may be reversed with consequent reversal

in the direction of translatory movement. If the turgor pressure should happen to be equal in the cells throughout the filament, according to the theory, no movement could occur. It is not clear just how suction pressure could be converted into mechanical force sufficient to propel the organism. It should be mentioned here that plasmolytic experiments do indicate differences in the osmotic properties of the cells in different parts of a filament of *Oscillatoria*, for example, but a definite gradient along the axis has not been demonstrated.

Though no good evidence has been offered in favor of the surface tension theory of movement, it is apparent that surface phenomena are intimately concerned with the mechanism of movement (*cf.* Pfeffer, 1906). It is indeed possible that the superficial films of blue green algae, diatoms, crawling euglenas, amoebae, gregarines, etc. are all similarly activated by surface tension changes (*cf.* Schaeffer, 1917, 1920; Scarth and Lloyd, 1930). Coupin (1923), while observing the movements of *O. limosa*, came to the conclusion that osmotic exchange between the organism and its environment would cause modifications in the surface tension and therefore influence movement. Hansgirg (1883) appears to have been unaware of the importance which might have been attached to a study of the surface tension in his experiments with *Oscillatoria* filaments gliding in almond oil. Some such method of approach as that of van Honert (1932), who demonstrated the rapid movement of oleate in an ether-water interface, would seem to have the possibility of yielding fruitful results.

Presumably the mechanism of movement in *Oscillatoria* might be similar to that involved in the movement of a small glass tube filled with gum camphor, sealed at one end in a flame and placed lightly upon the surface of water. Under these conditions the glass tube, not unlike *Oscillatoria* in shape, glides rapidly forward in a direction parallel to the long axis and away from the end of lowered surface tension brought about by solution of the camphor. With the aid of a micro-manipulator and fine glass needles, the author has been able to cut filaments of *Oscillatoria* into two parts and to observe their movement simultaneously under a microscope. The severed portions of filament glide rapidly away from the cut ends where it may be supposed that surface active materials are set free into solution. Furthermore, it has been noted that dried specimens kept in the herbarium for many years will exhibit the characteristic gliding movement when placed in a drop of 10 per cent glycerine in water between a glass microslide and cover. These observations appear highly suggestive and may be interpreted as supporting the surface-tension theory of movement.

Many of the early naturalists were inclined to regard the moving Oscillariae as

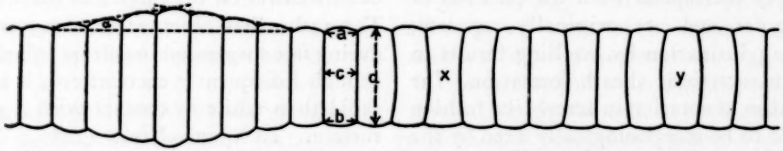

FIG. 4. THE LONGITUDINAL CONTRACTION WAVES IN OSCILLATORIA MAY BE INDUCED BY OSMOTIC PROCESSES CAUSING VARIATION IN THE SHAPE OF THE CELLS (CF. *x* AND *y*) AND PERHAPS ALSO IN THEIR VOLUME

Rhythmic changes in the dimensions (*a*, *b*, *c*, and *d*) of the cells throughout a filament have been observed; the magnitude of the transverse wave (measured by the angle α) lies on the border-line of visibility. (After Ullrich, 1926, 1929.)

"wurmförmig" animals which crawled by peristaltic contractions (Ingenhousz, Purkinje, Dujardin, etc. according to Hansgirg, 1887). Similarly, Cohn (1867) and Migula (1897) believed that movement was in some way brought about through contractility. Rhythmic contractions were noted in *Oscillatoria* by Phillips (1704) and later under dark field illumination by Crozier and Federighi (1924). Brand (1903*a*) showed that considerable contraction could be produced artificially in *Phormidium* by placing the filaments in hypertonic solutions of glycerine or KNO_3.

One of the principal champions of the contractility theory in recent years has been G. Schmid (1918, 1921, 1923) who claimed that normal rhythmic contractions of the cells cause the extrusion of the gelatinous stuffs along the entire filament, and also longitudinal and pendulatory movements. These contractions are believed to be set up by osmotic processes which proceed in waves along the filament. By employing solutions of sugar, KNO_3, NaCl, etc., Schmid found the longitudinal membranes capable of over 30 per cent turgor extension beyond the minimal value.

Careful analyses of the rhythmic contractions in *Beggiatoa* and in *Oscillatoria* have been made by Ullrich (1926, 1929) through the utilization of a stereo-photomicrographic method. In *O. sancta* at 24°C. the velocity of the waves was found to be 13 microns per second, the wave length 25 microns, and the velocity of translatory movement of the filament 0.684 microns, with the waves running against the direction of creeping. As a wave passed through a particular cell in the filament the width of the cell showed an increase and the length a decrease in size, the magnitude of the variations being on the borderline of visibility. In an 8 per cent sugar solution no waves were observed, yet movement of the filament continued. It was concluded by Ullrich that no definite direct relation existed between the observed waves and the speed of translatory movement.

MOVEMENT IN RELATION TO ENVIRONMENTAL FACTORS

For many years it was hoped to arrive at the truth through abstract reasoning, and the problem of movement in the Cyanophyceae was approached with an attitude of speculation. The newer point of view proposes to build up a theory of the mechanism of movement with the quantitative evidence derived from experiments in which the operating factors are controlled. A brief review of the pertinent data supplied by investigations dealing with movement in relation to different environmental factors will be given in the hope that additional quantitative information may be made available in the future.

Phototactic response in the motile Cyanophyceae was early described by Famintzin (1867), who found that *O. insignis* moved toward light of moderate intensity but turned away from direct sunlight. Bornet and Thuret (1876) noted a light response of hormogones of *Scytonema;* and positive "heliotropism" in *Oscillatoria* was reported by Borzi (1886). That movements of the blue green algae are more rapid in the light than in the dark has been the common belief (Hansgirg, 1883; Phillips, 1904; Pieper, 1913; Harder, 1920). However, Schmid (1921) claimed that light is unessential for the moving mechanism, since he found that *Oscillatoria* kept in the dark for 30 days was capable of movement when transplanted to 1 per cent agar in the dark. The speed of thiobacteria, as also their growth, appears to be independent of the

light intensity (Ruhland and Hoffman, 1925; Crozier and Stier, 1926).

For the growth of blue green algae in inorganic culture solutions proper conditions of illumination are highly important (Harder, 1922; Pringsheim, 1926). A pigmentary response to light of selected wave length and energy content has been claimed to result in complementary chromatic adaptation (*cf.* Gaidukov, 1903, 1906, 1923; Dangeard, 1911; Boresch, 1922). Harder (1923) noted that when *Phormidium faveolarum* was grown under different colored lights, it became chromatically adapted for the highest efficiency of assimilation under the existing conditions. Using equal intensities, he found that a wave length of incident light complementary to the color of the algae afforded better assimilation than did the same color of light. Harder (1917 *a*) also has shown that the percentage germination of *Nostoc* spores is proportional to the meter-candle-hours of exposure. The young hormogones of *Nostoc punctiforme* and of *Anabaena variabilis* responded in a positive manner by creeping over the surface of 1 per cent agar toward the source of illumination, and were thus obtained in pure culture by repeated transfers (Harder, 1917). When placed in the shade these algae assumed an heterotrophic existence upon the organic substratum.

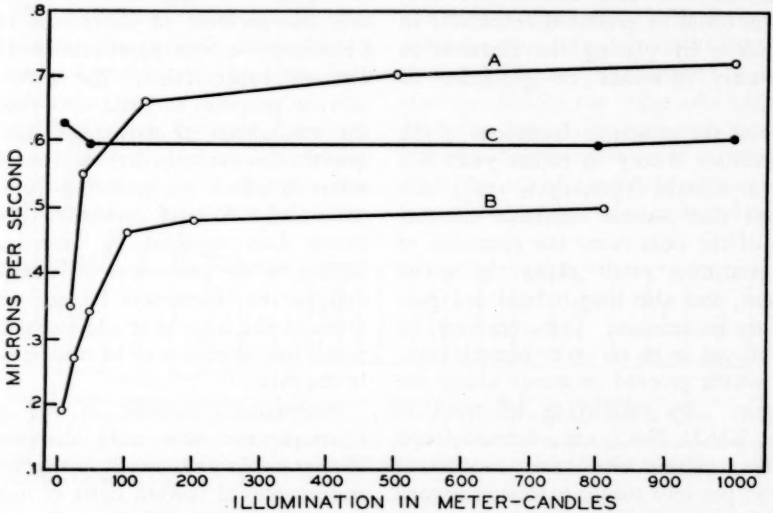

FIG. 5. TRANSLATORY MOVEMENT OF NOSTOC PUNCTIFORME UNDER DIFFERENT CONDITIONS OF ILLUMINATION FOLLOWING A PERIOD OF DARK ADAPTATION OF ABOUT 24 HOURS

The primary hormogones (*A* and *B*), germinated directly from spores, exhibit a marked acceleration in velocity with increasing light up to about 100 meter-candles; above this region the variation in response is less with change in the illumination. The movement of older hormogones (*C*) is not influenced much by variations in the light. In *A* the illumination was varied by the square of the distance; in *B* the light was modified by employing a rotating sector disc. (After Harder, 1918.)

The nutritional dependence upon light and the orientation with respect to the direction of the incident light are well-known phenomena in the blue green algae. The mechanism of their phototactic responses is not well understood, though considerable attention has been given to

the problem. Harder (1918) found a variation in the velocity of *Nostoc* filaments when subjected to different light intensities following a 24 hour period of dark adaptation. The speed of the primary hormogones of *Nostoc* increased with the light intensity between 5 and 900 meter candles. Up to 100 meter candles alterations in the intensity produced considerable changes in the rate of progression; above this intensity the effects were small. However, older hormogones were indifferent to variations in illumination between 5 and 2222 meter candles. It is not clear whether heat effects were entirely eliminated in these experiments and whether the direction of all incident light was controlled. It is probable that activity might be different under conditions permitting orientation with respect to the stimulus, and when such possibilities of orientation are excluded from the experiment.

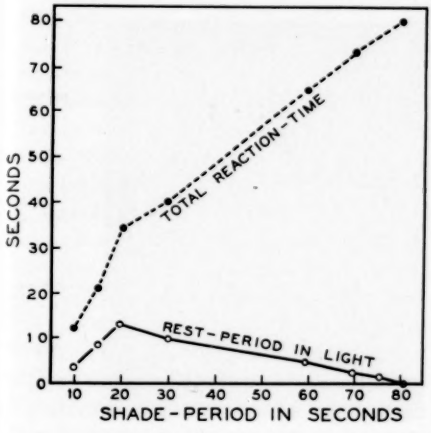

FIG. 6

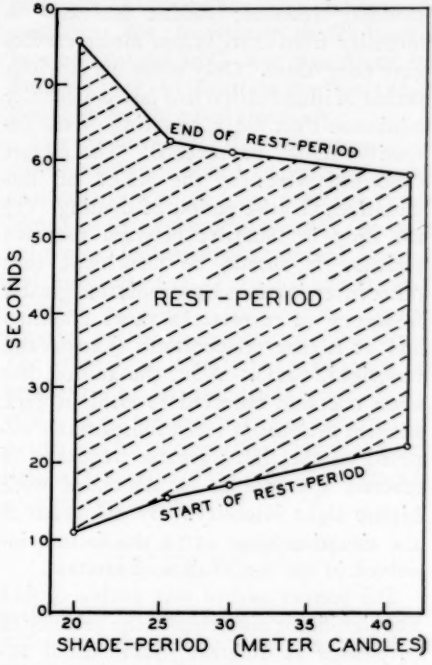

FIG. 7

FIG. 6. THE REACTION TIME (ORDINATE) REQUIRED FOR RESUMPTION OF MOVEMENT IN NOSTOC FILAMENTS AFTER QUIESCENCE HAD BEEN INDUCED BY EXPOSURE TO DIM BLUE LIGHT (EQUIVALENT TO DARKNESS ACCORDING TO HARDER, 1920) FOR VARIOUS LENGTHS OF TIME (ABSCISSA)

The filaments were first exposed to bright white light at 200 meter-candles for 2 minutes, then "darkened." When illuminated again with white light, movement was resumed after the lapse of definite periods of time up to 80 seconds. When the shade-period lasted more than a minimum of about 15 seconds, then reversal of direction always occurred, and the length of the rest-period (lower curve) in the succeeding light varied inversely with the duration of the shade-period. The total reaction time, measured from the beginning of the shade-period up to the resumption of movement in the light, appears to be directly related to the length of the shade-period. When the "darkened" period is greater than 80 seconds, movement is resumed upon subsequent illumination without any rest-period in the light. (After Harder, 1920.)

FIG. 7. THE REST-PERIOD IN CREEPING FILAMENTS OF NOSTOC IS INVERSELY PROPORTIONAL TO THE INTENSITY OF THE ILLUMINATION DURING A PERIOD OF SHADE

The organisms, accustomed to light of 800 meter-candles, were suddenly exposed to dim light in the range of 20 to 41.5 meter-candles (abscissa) and the time measured for cessation and resumption of movement (ordinate). (After Harder, 1920.)

Significant information as to the mech-

anism of reversal has been given by the same author (Harder, 1920) for *Nostoc* hormogones. Reversal of the direction of movement occurred when the intensity was suddenly lowered; sudden increases in intensity from 0 to 12,000 meter candles gave no reversal. Only when the previous period of illumination had lasted a definite minimum time did a lowering of the intensity result in reversal. The factors concerned were: (a) the period of illumination, (b) the period of shading, (c) the drop in intensity between the two periods. It should be mentioned that other investigations have indicated greater frequency of reversal in short filaments and at higher temperatures (Crozier and Federighi, 1924). Also, the author, has upon occasion observed reversal in dark adapted *Oscillatoria* when subsequently exposed to the light; greater frequency of reversal appeared to be associated with higher light intensity. By no means is the situation clear as to the factors involved in the mechanism of reversal.

The present author was unable to find any significant difference in the velocity of *O. formosa* at different illuminations between 0.01 and 26.2 foot candles after a period of 20 hours of dark adaptation. The temperature was definitely controlled at 22° ± a small fraction and the possibility of orientation was excluded from the experiment, since the incident light was perpendicular to the plane in which the organisms were allowed to glide. In other experiments with nine species of *Oscillatoria* it was found that the phototactic sign depends upon the species as well as upon the intensity of light. Negative phototaxis served to segregate *O. splendida* from other positively phototactic species associated with it in the same Petri dish. The diaphototaxis or orientation in such a manner that optimum absorption may be permitted has been found in the case of *Oscillatoria* filaments exposed to moderate light conditions (Pieper, 1913, 1915). In Figure 8 there is illustrated the autonomous orientation of a culture of *O. formosa*, the filaments being arranged in a position perpendicular to the direction of incident light. Other interesting experiments are in progress with *Oscillatoria* placed in nutrient solution in long glass tubes where the filaments glide spirally upon the inner surface toward suitable light sources.

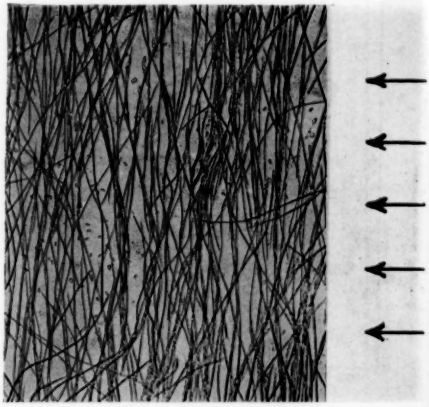

FIG. 8. AUTONOMOUS ORIENTATION OF THE FILAMENTS OF OSCILLATORIA FORMOSA IN A POSITION PERPENDICULAR TO THE DIRECTION OF THE INCIDENT LIGHT

Nienburg (1916) employed an ingenious technique for the observation of phototactic response in *Oscillatoria*. A very small beam of light was controlled by different sizes and shapes of apertures and was manipulated so as to illuminate one or both ends or only the middle of a single filament while creeping on a microscope slide. A change from light to darkness always caused reversal; a change from dark to light had no influence upon the direction of movement. Speed was apparently accelerated by increased light intensity (temperature not controlled?).

The conclusion was reached that all parts of a filament are equally reactive to light, but it was not possible to discover whether intensity or "direction of light" was operative in producing the photic responses.

There is certainly some definite relationship between the absorption spectrum of these organisms and their response to light. Absorption of the pigments of several of the members of the Oscillatoriaceae has been studied (*cf.* Engelmann, 1884; Sauvageau, 1908; Boresch, 1921 *a*, 1921 *b*; Wille, 1922), but little effort has been made to correlate movement with light absorption. Schmid (1923) thought that brown species (*O. Jenensis*) with a high proportion of phycoerythrin are negatively phototactic, and green species (*O. Cortiana*) positively phototactic. This assumption cannot be generally applied. Working with *O. formosa*, Pieper (1913, 1915) found positive phototaxis in white light of moderate intensity and negative phototaxis in strong tantalum-light and sunlight. In red and yellow light, at all intensities employed, there was strong positive response; within a definite optimum zone the filaments were oriented at right angles to the direction of the light. In dim green light the response was positive, but under increased intensity it became negative. The blue part of the spectrum seemed to cause a negative response. Pieper concluded that the manner of orientation depended upon the wave length, intensity, and direction of the beam of light.

Since the velocity of physical and chemical reactions bears a definite relation to change in temperature, the rate of biological processes in relation to temperature has been investigated by numerous workers in order to ascertain the nature of the mechanism involved. Harder (1918) studied the rate of linear translatory movement of *Nostoc* in relation to temperature and found the temperature coefficient to be $Q_{10} = 2$ at ordinary temperatures up to 30°C. The temperature coefficient for movement of *Oscillatoria* between 10 and 30°C. was also found by Schmid (1918) to illustrate the Van't Hoff Principle for chemical reactions.

In view of the fact that the temperature coefficient was deemed imperfect for the characterization of the processes concerned in this type of movement (as well as for other biological phenomena), Crozier and Federighi (1924) studied the critical thermal increment (temperature characteristic) of the movement of *Oscillatoria*. The velocity of translation was found to be controlled by the temperature (6 to 36°C.) in accordance with the equation of Arrhenius for irreversible chemical reactions. The value of the critical increment, μ, in this equation,

$$\frac{\text{velocity at } T_2}{\text{velocity at } T_1} = e^{\mu/2\left(\frac{1}{T_1}-\frac{1}{T_2}\right)}$$

was found to be 9,240. To quote these authors: "The velocity of movement is therefore regarded as determined by the velocity of an underlying chemical process, controlled by the temperature and by the amount of a substance (? catalyst) whose effective quantity at any moment varies within definite limits in different filaments of the alga." In view of a suspected connection between protoplasmic streaming and the movements of *Oscillatoria*, a comparison of the thermal increments for cyclosis in aquatic plants, and of the amoeboid movements of human neutrophilic leucocytes was made with the temperature characteristic for locomotion of *Oscillatoria*. It was concluded that these "are all influenced in a not very dissimilar way by the temperature, although the actual values of the several critical thermal increments seem distinct

and characteristic." Crozier and Stier (1926) studied the temperature characteristics for the speed of movement in *Beggiatoa* and *Thiothrix* and found that above 16.5°C. the value of μ for the former is 8,400 and for the latter 8,300. Below this temperature (*i.e.*, 16.5 −5°C.) *Beggiatoa* yielded a μ of 16,100, which indicated a different controlling influence in the lower temperature range. It is apparent that the visibly similar phenomena of motility in the blue green algae and the thiobacteria may be controlled by similar underlying chemical and physical processes.

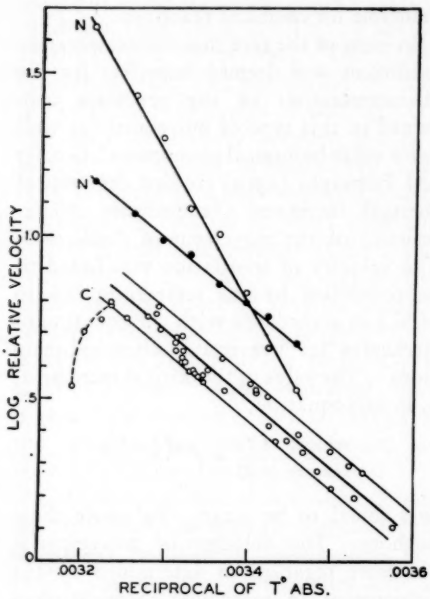

FIG. 9. THE VELOCITY OF TRANSLATORY MOVEMENT OF OSCILLATORIA IS CONTROLLED BY THE TEMPERATURE IN ACCORDANCE WITH THE EQUATION OF ARRHENIUS FOR IRREVERSIBLE CHEMICAL REACTIONS

The data indicated by *C* are taken from Crozier and Federighi (1924). Note that the extreme variates fall within lines parallel to that representing the slope of the set of values. At high temperatures (above 36°C.) the controlling mechanism appears to be disrupted, as indicated by the points breaking away from the characteristic slope. The other plots (*N*) are taken from the paper by Navez (1928).

The results of some work upon the movement of *O. chalybea* in relation to the temperature were published later by Navez (1928). What may have been two "temporary physiological races" yielded thermal increments (μ) of 9,450 between 8.2 and 26.2°C., and 21,700 between 13 and 35°C. respectively. The former value is significantly close to that obtained for another species of *Oscillatoria* by Crozier and Federighi. The values of μ about 20,000 are possibly concerned with hydrolytic reactions or processes H^+ catalysed; those below 10,000 might be connected with diffusion phenomena and surface action. Though it has not been possible as yet to identify the process controlling locomotion, it appears quite significant that this type of biological activity has been found to obey the law of temperature influence upon irreversible chemical reactions.

However popular in modern physiological research, the effect of dissolved substances upon cell permeability and the vital processes has not received much attention with respect to the Cyanophyceae. On the other hand, a great deal of attention has been given to this aspect of the problem in other organisms, such as amoebae, infusorians, leucocytes, etc. (Dale, 1913; Pantin, 1923, 1925–26; Fenn, 1922; Chambers and Reznikoff, 1926; Chase and Glaser, 1930). Information concerning movement in other organisms serves to throw considerable light upon, and is in certain instances perhaps directly applicable to the situation in the blue green algae. Further discussion of specific analogies must, however, be deferred at this time.

The osmotic properties and the permeability of several species of *Oscillatoria* have been studied, though no large body

of facts is available on the subject. Brand (1903) has pointed out that plasmolysis does not easily happen in this group, presumably because of the absence of vacuoles, and due to the elasticity of the cell membranes (*cf.* West and Fritsch, 1927). Prat (1921, 1925) found that the isosmotic concentration varied in different species between the limits of 0.8 to 1.5 per cent NaCl and 10 to 13 per cent saccharose. Species of *Oscillatoria* were plasmolysed in ment was more rapid in relatively dilute Knop's and in relatively concentrated NaCl and saccharose solutions. Schmid (1923) found that the osmotic pressure in the cells of *O. Jenensis* was lower than in other plants for which data were available with the exception of slime molds. According to Prat recovery from plasmolysis was more rapid in the case of monovalent metals than divalent (using the chlorides in all cases). No deplasmolysis with

TABLE 1

The Relative Rates of Deplasmolysis of Oscillatoria in Various Salt Solutions as an Indicator of the Permeability. (o = Recovery in 30 Seconds to 5 Minutes. + = Deplasmolysis in Concentrations Below M/3 in 10 to 30 Minutes, and in Higher Concentrations from 30 to 50 Minutes. ++ = More than One Hour Required.) (After Prat, 1921)

CATIONS / ANIONS	Li	K	Na	Mg	Ca	Sr	Ba
Cl	+	o	+	++	++	++	++
NO_3		+			++	+	+
SO_4		+	+++	++++			
H_2PO_4		+					
HPO_4		o					
PO_4		+					
CNS		∞					

TABLE 2

The Relation of Velocity of Movement to Turgor Pressure and Diameter of the Filaments in Several Species of Oscillatoria (after Krenner, 1925)

SPECIES	SIZE	SPEED	MOVEMENT IN SUCROSE SOL.	MOVEMENT INHIBITED	ISOTONIC SUCROSE SOL.	TURGOR IN ATMOSPHERES
O. Frohlichii	broad	slow	5–6.5%	8.0%	24.0%	16.63
O. curviceps	medium	slow	6–8.5%	9.0%	28.0%	19.40
O. tenuis	narrow	fast	17%	20.0%	37.5%	25.98

1.6 to 1.8 per cent KNO_3 and in 1.0 to 1.1 per cent NaCl. When the concentration of a saccharose solution was slowly increased by evaporation, the immersed algae were able to withstand much higher values than under ordinary conditions. The threshold concentration permitting movement in the species of *Oscillatoria* studied by Prat was 1.5 per cent Knop's solution, 1 per cent NaCl, and 13 per cent saccharose. Below the threshold, move- $MgSO_4$ or sugar was obtained, indicating impermeability of the cell membrane to these substances.

Since the manner of movement in the thiobacteria is not unlike that in the Cyanophyceae, the recent investigations of Ruhland and Hoffman (1925) and Ruhland, Ullrich and Yamaha (1932) upon the permeability of *Beggiatoa mirabilis* are of interest in this connection. These authors have concluded from plasmolytic

experiments with a long list of substances that penetration of large organic anions is inversely proportional to the radius of the ion, which lends support to the concept of an ultra-filter mechanism for the permeability.

Attempts have also been made by several writers to correlate speed with the osmotic pressure and size of the filaments. According to Correns (1897) the velocity is proportional to the diameter (with some exceptions). Recently Krenner (1925) has reported that the narrow and rapidly moving filaments of *O. tenuis* have an osmotic pressure of 25.9 atmospheres (using cane sugar); the broad and less rapid filaments of *O. curviceps* and *O. Frohlichii* have a pressure of 19.1 and 16.6 atmospheres respectively. The conclusion was therefore put forth that velocity of translation is proportional to the osmotic pressure of the alga, and varies inversely with the diameter of the filament. Whether or not this statement will hold true, the evidence is quite convincing that the greater the osmotic pressure within the cells, the higher the concentration of solution in which the organisms can continue to move.

It is worthy of note that no relation exists between length of filament and velocity of motion (Crozier and Federighi, 1924; Castle, 1926), though there has been a suggestion of some correlation between length and frequency of reversal. Krenner (1925) claims that there is a minimum length below which movement does not occur in each species. Thin species (*O. natans*, *O. tenuis*, *O. tenerrima*) with relatively high osmotic pressure are held to be capable of movement if more than 16–21 cells comprise the filament; in larger species (*O. princeps*, *O. Frohlichii*) with lower osmotic pressure, a minimum of from 45–50 cells is required to permit movement. In the thiobacteria, the larger individuals were observed to move faster than the small ones (Crozier and Stier, 1926). It was suggested by these authors that some relation may exist between velocity and the surface/volume ratio in all these cases.

Nutritive conditions appear to affect both growth and movement by a direct influence upon the elaboration of food materials and upon the preservation of equilibrium in the vital structures of the cell. The long forgotten opinion of Wolle (1887) that growth and movement in the Cyanophyceae are identical is of course not strictly true, though the two are intimately interrelated. In an investigation of the optimum culture conditions for blue green algae, Maertens (1914) found that properly balanced proportions and concentrations of dissolved salts and a slightly alkaline reaction are required. Directions for the preparation of culture media suitable for the growth of Cyanophyceae may be found in the papers of Pringsheim (1913, 1926), Maertens (1914), and Kufferath (1929). Statements in the literature concerning the deleterious effect of an acid environment appear to be correct, a negative "chemotactic" response to acids hav-

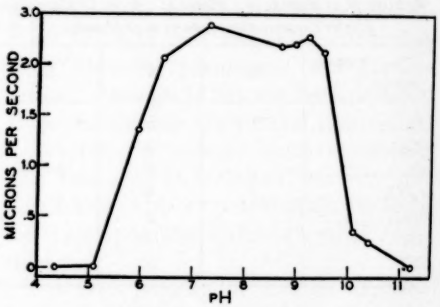

FIG. 10. MEAN RATES OF TRANSLATORY MOVEMENT OF OSCILLATORIA FORMOSA AFTER IMMERSION FOR ABOUT 10 HOURS IN CULTURE SOLUTIONS OF DIFFERENT pH

Each point represents the mean value for 10 filaments; all data are taken from a single series representing a typical experiment. Movement appears to be sustained in the region pH 6.4 to 9.5.

ing been observed by Fechner (1915) and the lethal effect of acids having been noted by Schmid (1923). In recent experiments with *O. formosa*, movement was found to be sustained in inorganic culture solutions within the range pH 6.4–9.5; above and below these limits inhibition of motion was marked (Burkholder, 1933).

Many other phases of the subject remain practically untouched. For example, the analysis of movement under various conditions of O_2- and CO_2-tension; the effect of salts, and antagonism; orientation to light in relation to the absorption spectrum; the effect of organic nutrients; etc. Celakowski (1898) reported movement of *Oscillatoria* in the absence of free oxygen and it has been suggested by Coupin (1922) that moisture and the oxygen tension are of great importance but, as in the case of so many other factors bearing upon this problem, no quantitative data are as yet available. The author has found that movement in the light is enhanced by the presence of bicarbonates in solution, and that the phenomenon of antagonism is demonstrated by differential movement of *Oscillatoria* in single and mixed salt solutions (NaCl and $CaCl_2$) of proper concentration. Furthermore, the addition of small amounts of glucose to inorganic culture solutions was found to exert a positive effect upon the movement of *Oscillatoria* which had been kept continuously in the dark for several days.

In controlled experiments, Schmid (1921*a*) claimed that *Oscillatoria* exhibits neither hydrotropism, stereotropism, nor geotropism. The absence of geotropic response had been reported earlier by Stahl (1884). The interesting behavior of cyanophyceous colonies as units has been commented upon by several authors. For example, Prat (1925) found that the individual filaments tended to aggregate in lower concentrations of salts; in moderately concentrated solutions the filaments glided about separately. The experiments of Funk (1920) with colonies of *Oscillatoria* in glass tubes showed that the filaments gather closely together at low temperatures or while under the influence of an electric current. Also the individuals tend to scatter in the light and cluster together in the dark. Slight mechanical agitation is known to stimulate a more rapid rate of movement but if carried too far will depress activity of the organisms (Crozier and Federighi, 1924; Schmid, 1918).

SUMMARY

In the filamentous blue green algae, three types of movement have been recognized: linear translation, axial rotation, and oscillation. Linear translation appears to be particularly well suited for study in relation to controlled variables which influence the direction and velocity of movement. Different authors have at various times ascribed the mechanism of movement to growth, the presence of cilia, osmotic currents, the excretion of gelatinous materials, modifications of the surface tension, and peristaltic contractility of the cells. Among the various species of *Oscillatoria* the rate of linear progression appears to be related to the osmotic pressure of the cells and the diameter of the filaments. Other conditions being favorable, the intensity and wave-length of the incident radiation are important in determining the direction and perhaps also the speed of movement. Furthermore, the velocity of linear translation has been found to illustrate the Arrhenius law of temperature influence upon chemical reactions. Numerous investigations of movement in relation to different factors have provided interesting data, but as yet no satisfactory explanation of the mechanism has been offered. The history and present status of the problem have been reviewed in the hope that additional information may be made available in the future.

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MICROBIOLOGICAL ACTIVITIES AT LOW TEMPERATURES WITH PARTICULAR REFERENCE TO MARINE BACTERIA

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ALTHOUGH it is frequently stated in the popular as well as in some scientific literature that the ocean floor beyond the continental shelves is barren of bacterial life, primarily due to the lack of food and the prevailing low temperature and high hydrostatic pressure, investigators have almost invariably demonstrated the presence of an abundant bacterial flora in bottom deposits wherever critical analytical procedures have been applied. In fact, there are usually from ten to ten thousand times as many viable bacteria per gram of mud as there are in a corresponding quantity of water in any superimposed strata. While nearly all of the studies on marine bacteria to date have been made in relatively shallow water near land, a few workers have recovered significant numbers of living microörganisms from mud collected at depths of a mile or more. However, the recovery of organisms from such depths is by no means incontrovertible proof that these organisms are biochemically active in such an environment, because they may be merely passive inhabitants which have settled from above and have been preserved by the cold.

Inasmuch as over four-fifths of the ocean floor exceeds one mile in depth and has a temperature colder than 3°C., it is of importance to know if bacteria and kindred microörganisms survive and if they are physiologically functional under such conditions. Our knowledge of the activities of bacteria in the sea is very fragmentary, but the few investigations which have been made indicate that bacteria probably play an important rôle in the sea. They themselves are consumed as food by many small marine animals and, also, by their activities they produce plant nutrients. They are the responsible agents for many of the chemical and physico-chemical changes which occur in sea water or on the ocean bottom, and they may be of geological importance (cf. Bavendamm, 1932; Benecke, 1933; Waksman, 1934).

Experimental evidence indicates that for practical purposes the hydrostatic pressure of deep water is not inimical to microbial well-being. Tremendous pressures are encountered on the sea bottom but bacteria have been shown to tolerate far greater pressures than occur even in the most abyssal depths. Chlopin and Tammann (1903) found that pressures up to about 2900 atmospheres, or approximately three times that found in the ocean, failed to harm bacteria, yeasts or molds, although individual organisms differed greatly in their susceptibilities to higher pressures. In the experiments of Larsen, Hartzell, and Diehl (1918), non-spore-formers survived at 3000 to 6000 atmospheres and then, at these pressures, compressed gases, such as carbon dioxide, or the sudden release of pressure were found to be more detrimental than pressure itself. The actual recovery of bacteria by Certes

(1884), and recently by Carey and Waksman (1934), from depths near 5000 meters proves that neither the pressure encountered (approximately 500 atmospheres) nor its release, effected by bringing the mud samples to the surface, injures the viability of the microbes.

BACTERIAL RESISTANCE TO COLD

While modern methods of food preservation are based upon the principle that refrigeration prevents or materially retards microbiological activity, it has been recognized for a long time that sub-zero temperatures do not necessarily kill bacteria. According to evidence reviewed by Hampil (1932) *Eberthella typhi* survived −153°, and *Vibrio cholerae* survived −183°C, for 7 days; *Corynebacterium diphtheriae* survived −190°C for 10 days, and *Gonococcus* lived after 24 hours at −195°C. As a general rule, water and soil microbes are more cold-tolerant than these delicate pathogens. In the opinion of Keith (1913) freezing does not harm bacteria unless they are mechanically injured by ice crystals, but on the contrary low temperatures actually favor bacterial longevity by diminishing destructive metabolism. In fact, recent work indicates that in the case of at least certain bacteria, life may linger until absolute zero (−273°C) is reached, since some are unharmed by cooling to −252°, the temperature of liquid hydrogen.

McLean (1918) has described four species of bacteria which he isolated from the ice, snow, and frozen algae of Antarctica in locations where possibilities of airborne contamination are most remote. Here the mean annual temperature is about −20°C, and temperatures as low as −60° are not uncommon. He believes that some bacteria actually prefer to grow in ice where they learn to live within the liquid sludge of cryohydrates which circulates between the crystals of ice. Issatchenko (1914) has reported finding a rich, varied, and vigorously active bacterial flora in the glacial Arctic. At the present time Paul A. Siple, biologist of the Byrd Antarctic Expedition II, is making observations on the distribution of bacteria in the air, ice, water, mud and animal life of the South Polar regions.

BACTERIAL GROWTH AT LOW TEMPERATURES

Granting that bacteria are not killed by cold, to what extent are they functional at the near-zero temperatures typical of oceanic abysses? While investigating the effects of storage on the multiplication of bacteria in water samples, Ellison, Hackler and Buice (1932) observed that bacteria continue to multiply in iced samples. Similar studies conducted by ZoBell and Feltham (1934) showed that samples of sea water held at near 0°C for a few hours exhibited an increase in the total number of bacteria present, although there was a decrease in the number of predominating species, probably due to the selective action of the colder temperatures. The same investigators later noted a twofold increase in the bacterial population of mud samples after storage at near 0°C for three weeks. Fischer (1888) described fourteen different species of bacteria from water and soil of Kiel harbor which were capable of growing at 0°C. Conn (1914) has shown that, while many factors are involved in the increased bacterial counts of frozen soil, the facts indicate an actual growth of the bacteria therein.

Further evidence of the multiplication of bacteria at low temperatures is furnished by Damon and Leiter (1927) who point out that there is a real danger of human intoxication from certain members of the *Salmonella* group which can multiply in frozen foods. The literature

is replete with accounts of bacteria which grow in foodstuffs at temperatures ranging from a few degrees below zero to a few degrees above. Although milk at 0°C is a mass of floating ice crystals Pennington (1908) noted that bacteria continue to reproduce extensively in the serum. Prescott, Hale and White (1931) have reported that the disagreeable odors and slimy coatings on beef in cold storage are produced by microörganisms which grow readily at temperatures only slightly above the freezing point. Redfort (1932) observed the multiplication of bacteria on fish stored at −11°C after 16 months.

When long periods of time are required before multiplication starts, adaptation of the bacteria to the lower temperatures may be taking place. Such acclimatization to temperatures assumed to be inhibitive has been reported by Prescott and Bates (1931). According to Kluyver and Baars (1932) most bacteria in nature are "pluripotent" or readily adaptable to unfavorable environmental conditions. As one example they mention *Vibrio thermodesulfuricans* (Elion) which is normally characterized by its thermophilic (50°–60°C) requirements but which can be easily acclimatized to much colder temperatures and in so doing becomes indistinguishable from *V. desulfuricans* (Beijerinck). Another manifestation of adaptation is recorded by Waksman (1929) who quotes Mischustin as showing that bacteria isolated from soils of colder climates are capable of growing at lower temperatures than those from warmer climates.

In their excellent contribution to the question of the minimum temperature for bacterial multiplication, Horowitz-Wlassowa and Grinberg (1933) concluded that the number of microbes which will reproduce at −4° to −7°C is appreciable. They examined about 75 organisms including many common bacilli, cocci, yeasts and molds, most of which they found would grow at 0° to −7°C. In some cases it required as long as 136 days for growth to become perceptible, although a few microörganisms exhibited good growth in a week at −3° to −7°C.

Many marine bacteria have been described which continue to be active at sub-zero temperatures. Forster (1887) isolated a photogenic species from luminescent fish which reproduced at 0°C, and later (1892) he found that bacteria which will grow at low temperatures are quite widely distributed in water and soil. Zirpolo (1929) who has extensively studied the physiology of bioluminescence found that *Pseudomonas pierantonii* grew readily at −4°C although the optimum temperature for multiplication and light production was around 33°C. This bacterium was not killed nor was luminescence prevented at a temperature of −192°C produced with liquid air.

In Bedford's (1933a) comprehensive investigations on the temperature range of growth of marine bacteria, all except six of the 71 different species which he examined grew at 0°C or below in 136 days, after which time the experiment was terminated. Ten of the bacteria had multiplied at −7.5° and 12 others at −5°C. Lower temperatures were tried but not successfully because at −10° the frozen media crystallized to such an extent that results were obliterated.

While no efforts have yet been made at the Scripps Institution to ascertain the lowest temperature at which multiplication occurs, work in our laboratory shows that the majority of the bacteria isolated from the sea reproduce freely at 0° to −4°C. A total of 88 different species of marine bacteria isolated from bottom deposits or sea water have been observed, and all except 12 of them have shown evidence of growth after three months'

incubation at this temperature. Some of them, one the etiological agent of a fish disease (Wells and ZoBell, 1934), produce a perceptible turbidity in appropriate sea water broth after 7 days at −2°C. In another series of experiments on mud samples collected at a depth of 1300 meters where the temperature was 6°C, similar dilutions were plated on nutrient agar and incubated at temperatures ranging from −4° to 25°C. After 4 days' incubation the average count for those held at 25° was 49,000 bacteria per gram of mud, 41,000 for those held at 18°, and those at −4° showed no macroscopically visible colonies. At the end of a week counts on the 25° series became unreliable due to merging of rapidly growing colonies, the 18° series had increased to an average of 46,000, and the −4° series showed 8,000 colonies per gram of mud. The −4° series gave an average count in two weeks of 22,000 and in four weeks of 29,000 while, the colonies were slowly increasing in size and in pigment intensity.

The evidence seems conclusive that a large proportion of the bacteria isolated from the sea can grow at the lowest temperatures found in the depths of the ocean. Furthermore, most marine bacteria are more or less eurythermic, or capable of growing over a broad range of temperatures (from approximately 30° down to such a temperature that the physical constitution of the substrata becomes unfit for their continued metabolism). The majority of the marine bacteria observed by Bedford (1933a) had a temperature range of growth from −5° to 30° or 37°C. It is of interest to note that for most marine bacteria on which information is available their optimum temperature is very near their maximum, and considerably higher than their minimum. For non-spore-formers the lethal temperature is only a few degrees higher than the maximum at which they grow. This is illustrated by *Achromobacter ichthyodermis* described by Wells and ZoBell (1934) which, following primary isolation, grows at −2°C or perhaps lower; its optimum is about 25°; its maximum 30°; and 32° is lethal.

BIOCHEMICAL ACTIVITIES OF BACTERIA AT LOW TEMPERATURES

Although many bacteria reproduce freely at sub-zero temperatures, in the experience of Horowitz-Wlassowa and Grinberg (1933) demonstrable biochemical activities are at a low ebb and the psychrophiles are very feebly proteolytic and lipolytic at temperatures below 0°C. Unfortunately, there is little information available on the minimum temperatures for enzymatic activity. However, it is quite probable that, in general, enzyme action is not entirely suspended until all interstitial water is removed by its solidification due to freezing. The work of Talyract (1901), Glage (1901), and many others proves that proteolytic enzymes elaborated by bacteria are definitely functional at sub-zero temperatures, in some cases as cold as −9°C, as manifested by the spoilage of refrigerated foodstuffs. Sanborn (1930) has described several marine bacteria responsible for the decomposition of fish in cold storage, some of which vigorously continue their proteolytic activities at −5°C. It was the opinion of Browne (1917) that autolysis rather than bacterial action plays the most important part in the initial stage of fish decomposition during storage in ice but, regardless of the source of the enzyme, proteolysis was relatively rapid near 0°C. Bedford (1933b) has shown that the decomposition and red discoloration of refrigerated halibut is due to marine chromogenic bacteria which are functional at 0° to −5°C and perhaps at lower tem-

peratures. Evidence is recorded by Rubentschik (1925) of bacteria from the Odessa limans which multiply freely, liquefy gelatin and form ammonia at temperatures ranging from −2° to 0°C. He described two new species, *Urosarcina psychrocarterica* and *Urobacillus psychrocartericus*, which split urea at −1.25° to −2.50°C. Berry (1934) has noted the multiplication of yeasts and their fermentation of sugars at −2.2°C.

During the last year the writer has observed several types of biochemical processes which are activated by marine bacteria incubated at from 0° to −2°C. Among these physiological activities may be mentioned the liberation of ammonia from peptones, the decomposition of urea, the liquefaction of gelatin, the fermentation of glucose, the hydrolysis of starch, and the oxidation of ammonium to nitrites. The latter reaction required 27 weeks before it became certain that nitrification was occurring, although large inocula of active nitrifiers were used. In general, the endothermic nitrogenous reactions are comparatively slower at the low temperatures than are the exothermic hydrolytic processes. While in all cases the speed of the reactions is extremely slow, there is an obvious acceleration after the first few weeks of incubation, probably due to adaptation of the bacteria to the cold.

In view of the foregoing information it seems both safe and logical to assume that, as far as the temperature is concerned, bacteria can multiply and activate biochemical changes in the coldest waters of the ocean. Many species of marine bacteria have been found to be active at temperatures even colder than the freezing point of sea water (−1.9° at a salinity of 35 per thousand). Microbiological activity may be quite appreciable on the ocean floor because the temperature of a large proportion of the latter ranges from 2° to 3°C., several degrees warmer than the known temperature at which many bacteria have been shown to be functional. While the action of bacteria may be very slow at near-zero or sub-zero temperatures, the total results may be of vast significance in the ocean because of the almost unlimited time and the relative slowness of other processes which are taking place concurrently. For example, the rates of many geological processes are far too slow to be measurable, but the accrued results from thousands or millions of years' activity are stupendous. Furthermore, in the case of the bacteria it is possible and quite probable that those which inhabit the abyssal depths have adjusted themselves so that they are far more efficient than they seem to be under artificial laboratory conditions. Such adaptation to environmental conditions is more or less universal in the plant as well as the animal kingdoms. However, exact knowledge as to what extent bacteria and related microorganisms are of importance on the ocean floor must await additional information concerning the nutritional, physico-chemical, and biological conditions which exist there.

Certainly the speculations of some writers that the organic matter which sinks to the deep ocean floor is there permanently preserved from decomposition by bacteria is not tenable with the known facts. It is doubtful if the dead bodies of either plants or animals are acted upon extensively by bacteria before the former are devoured by the scavengers of the sea. It must be recognized, though, that there would be many waste products which are unfit as food for animals, and it is primarily these waste products which, constantly raining from above, must be transformed by bacteria into something useful. Otherwise, there would be a con-

tinual drain on the elements essential to protoplasm which would eventually upset the balance in nature. It is probably on the sea bottom that these waste products are transformed by bacteria into plant nutrients or converted into bacterial cells which are in turn eaten by animals. Thus, the cycle of life in the sea is maintained in spite of high hydrostatic pressure or low temperatures.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THIS PROGRESS. *The Tragedy of Evolution. By Bernard Acworth. Rich and Cowan, London.* 7s.6d. net. $7\frac{1}{4}$ x $4\frac{3}{4}$; 334; 1934. Captain Acworth of the British Navy, author of *The Navy and the Next War* and *Navies of To-day and To-morrow*, not liking the present trends in politics, economics, engineering, industry, society, science, religion, or what have you, and attributing these tendencies to the influence of the evolutionary viewpoint, proves to his own satisfaction that evolution never occurred, that God created each species *ad hoc* substantially as described in the book of Genesis.

In his rather cavalier treatment of the geological evidences of evolution his principal authorities are Sedgwick, who died in 1873, and Dawson, who died in 1899. Captain Acworth, with his passion for the Absolute, would no doubt reply that the date when a scientist reaches a conclusion bears no relevance to its truth, that truth is the same yesterday, to-day and forever. But the conclusions of a scientist at any given date must be based on the evidence then available; if new evidence is discovered the old conclusion may have to be changed. The argument from the geological evidence is not merely "that because man appeared after fish he is therefore descended from fish" but that there is a graded series of fossil and living forms from fish to man and that as more and more fossils are discovered the gaps in the series are more and more completely filled. There is of course no question of proving past evolution in the same sense that we prove the existence of Julius Caesar. But there is an equal lack of historical testimony to special creation. If no one saw the evolution of reptiles into mammals, it is equally true that no one has seen God create a species. The authors of the accounts on which Genesis is based do not claim to have been present at the creation. On the other hand, as Conklin points out in his recent Penrose lecture,

> Nearly a score of new species of plants, having all the characteristics of true Linnaean species, have been artificially produced by hybridization or operations under experimental conditions with consequent changes in chromosome numbers and associations. These new species are fertile *inter se*, but are sometimes sterile when crossed with either one or both of the parent species, thus fulfilling the strictest definition of true species as laid down by many systematists.

We have thus definite evidence for experimental production of new species.

Many of Captain Acworth's arguments, such as his repeated statement that Mendel disproved natural selection, are no doubt attributable to misunderstanding of a subject with which he is not familiar. However, in other passages his tone is that of a barrister determined to convince the jury at all costs. We fear that he belongs in the same category as Bishop Wilberforce, "a man of restless and versatile intellect, who, not content with success in his own sphere of activity, plunges into scientific questions, with which he has no real acquaintance, only to obscure them by an aimless rhetoric, and distract the attention of his hearers from the real point at issue by eloquent digressions and skilled appeals to religious prejudice."

THE MEN BEYOND MANKIND. *A Study of the Next Step in Personal and Social Evolution. By Fritz Kunz. Rider and Co., London.* 5 shillings net. $7\frac{1}{4}$ x $5\frac{1}{8}$; 236; no date.

For a delightful, billowy ride the good ship Evolution takes wings of the lightest philosophical fabric. As it is with theosophical thinking, the hard won theories of science are spun out and stretched to make a bridge that reaches from the innermost of man to the limits of the imaginable.

The style is straightforward, simple, and sincere, making delightful the clever characterizations of our typical social and mental absurdities. If one were not inclined at times to stop and look for the parting of fact and fancy the excursion would be perfect, for the thesis is that there is no parting and all is unity.

We learn that we are in the fifth phase of human evolution, the intellectual phase, characterized by the accomplishments of the Aryan race. The next, the sixth evolutionary billow of humanity, is destined to come from a fusion of races in America, Australia or New Zealand. If these countries fail by misguided leadership Russia is the reserve selection of nature to fulfill the initiation of the age of intuitive brotherhood. Stupid social and economic systems as typified by our legal and financial organizations, will have been sloughed off, and the leisure gained by the elimination of economic cruelty will allow completion of the arts, scientific knowledge, and theosophy. We venture the corollary that the moiling types of mankind will have long since died out from sheer boredom. The author points out that we can already see a terrible *ennui* affecting many young people who have leisure without intellectual development. We quote: (pp. 215–216).

"The world will then be a place of beauty, filled with people who have a desire to learn, and not a crass democracy where everyone thinks himself theoretically as good as his fellow, and, in fact, just a little better." And again: "There are some seven groups of ductless glands altogether, representing the seven aspects of nature. Hence, all the other worlds are partially focused in the ductless glands, from the higher point of view, if not from the doctor's point of view."

This is partly to say that there are seven phases to human evolution. The seventh phase is the spiritual realm of free souls and the grandeur of that area has not yet been completely imagined for mankind is only far enough advanced to dimly visualize the sixth area and is still confronted with the task of making that evolve. We are in the so-called trap of free will and cannot refrain from being conscious, so why hinder the progress of the coming epoch when all true knowledge will help toward its timely flowering?

POUR ET CONTRE LE TRANSFORMISME. *Darwin-Vialleton. By A. Mignon. Masson et Cie, Paris.* 50 francs. 9 x $5\frac{1}{2}$; 521; no date (paper).

The title of this book clearly reveals the object of the author: a comparison of Darwin's theory with that of the late Professor Vialleton. The latter in an attempt to base his theory only on paleontologic and embryologic evidence admits an evolution of species but denies transformism. This viewpoint is based essentially on the following considerations: (1) transitional species have not been discovered; *Archeopteryx* for example, he states, is a bird and nothing but that; (2) the earliest example of some species is organically more complex than the descendants now existing; (3) the homology of certain organs and ontogenesis cannot be associated with phylogenesis. Vialleton's belief is that each species springs forth in some geologic epoch, fully armed like Minerva, to evolve, decline and die. The time of its "birth" and form of evolution is dependent on an unspecified "action intelligente."

The author, in a manner deserving great praise, presents fully the elements of both theories placing well in relief their weaknesses. He proceeds also to level criticism at some neo-Lamarckians and at the geneticists who are advocates of the mutation theory. For him, the theory of the former is a scientific credo based on affirmations, and not facts, the latter have accomplished nothing because so far "la mouche drosophile, pour torturée qu'elle soit, demeure une mouche." Still it is from the laboratories that he hopes for future enlightenment.

A book unreservedly recommended for all those who firmly believe in some theory of evolution.

EARLY FORERUNNERS OF MAN. *A Morphological Study of the Evolutionary Origin of the Primates.*

By W. E. Le Gros Clark. William Wood and Co., Baltimore. $5.00. 10 x 6⅝; xvi + 296; 1934.

The author believes that the most profitable method of determining the line of evolution which culminated in man is in studying, in proper perspective, the evolutionary development of the whole group of primates. Thus can be noted the "trends of evolutionary development which became manifested in the early generalized Primates, and by following them up, recognize which particular trends led to the line of evolution which culminated in Man." In this volume will be found a comprehensive survey of the results of studies in comparative anatomy and palaeontology of members of the primate group arranged under such headings as: The evidence of the skull, the evidence of the teeth, the evidence of the brain, etc. There are also sections on the relation of the tree shrews to the primates, and on the distribution in space and time, and evolutionary radiations of the primates. In the latter chapter is emphasized the importance of recognizing the principle of orthogenesis in any philosophical study of the evolution of the human race. The investigator will find this discussion of the early forerunners of man particularly useful in pointing out the gaps where future studies should be made. The book is well illustrated and documented and contains an index.

THE MISSING LINK. *Studies in Genesis.*

By Spencer H. Elliott. Group Publications, London. 2s. 6d. net. 6⅜ x 4; 143; 1934.

The curious thing about the title of this book is that comparatively little is said in the book itself about the Missing Link. The "Genesis" of the subtitle is the first book of the Old Testament, not the phylogenesis of the biologists. For the most part Canon Elliott is concerned with drawing moral and spiritual lessons in the usual clerical manner from the stories of Adam and Eve *et al.* However, in the first chapter he does consider evolution briefly and concludes that mankind has

> a twofold origin. On the physical side we may trace back our descent through the various stages of life to the dust of the ground from which we were formed; and we may have to admit that we have kinship with the ape, although we are not descended from him. But we have another pedigree which no ape can share—the human spirit which we trace back to God, Who breathed into mankind that which makes a man a living soul.

This, he considers, is proved by the greater mental endowment of man. "The child of two, counting his toes, has already proved himself to belong to a different order from that of the chimpanzee." Yet the child of two has developed without any discontinuity from the child of two weeks, who certainly shows no higher mental capacity than the chimpanzee. May not phylogenetic mental development have followed a similar continuous course?

THE DINOSAURS. *A Short History of a Great Group of Extinct Reptiles.*

By W. E. Swinton. Thomas Murby and Co., London. 15 shillings net. 8½ x 5½; xii + 233 + 25 plates; 1934.

Probably few Americans outside of the scientific group are aware that the region extending from Colorado and Utah north through Red Deer River and Edmonton areas of Canada has contributed the most important finds as well as the most numerous specimens of dinosaurs. The writer of this book, an authority on dinosaurs, is on the staff of the Natural History Section of the British Museum. He gives to the general reader a well rounded picture of all that exploration and research have contributed concerning these ancient reptiles. Even a chapter on disease is included. The numerous illustrations throughout the volume are well chosen. Each section concludes with a bibliography and in the two appendices are given (a) a list of British dinosaurs including author, hori-

zon, locality, reference and type specimen; and (b) a glossary and notes. There is a detailed index.

THE CONSTRUCTION OF MAN'S FAMILY TREE.

By Sir Arthur Keith. Watts and Co., London. 1 shilling net. $7\frac{1}{8}$ x $4\frac{3}{4}$; vi + 54; 1934.

In this little book Sir Arthur Keith traces the history of the various family trees by which zoologists since Haeckel have reconstructed the ancestry of man. He concludes that in broad outline Haeckel's schematization has been borne out by later discoveries of fossil primates, that the resemblances between man and the great anthropoids are more reasonably explained by the descent of man from a common anthropoid stock than by convergent evolution, and that Klaatsch's theory that the anthropoids are degenerate forms of humanity runs counter to the geological record.

GENETICS

ENVIRONMENT AND GROWTH.

By Barkev S. Sanders. Warwick and York, Inc., Baltimore. $4.00 + postage. 9 x $5\frac{7}{8}$; xviii + 375; 1934.

This painstaking study shows, in the author's opinion,

> that the deductions of the Pearson School from correlation studies are untenable, not merely in respect of growth but in all other spheres where an attempt has been made to evaluate the contribution of heredity on environment through this methodology without the use of other correctives.

Furthermore the author tells us that:

> The present study was therefore undertaken for the sake of a more intensive and extensive analysis of the evidence bearing on the relative contributions of heredity and environment to physical growth and development, and a more rigid determination of the tenability of the deductions from correlation studies. The organized data presented in the subsequent pages do not sustain the claims of extreme hereditarianism, more specifically the deductions of the Pearson School which deny the importance of milieu on ontogenetic traits.

These are strong words, and Professor Pearson is a considerable person, who has collected and analyzed probably more quantitative data pertinent to the problem of nature and nurture than any other person who has ever lived. It is not unreasonable, therefore, to examine the basis upon which rests Dr. Sanders' alleged demolition of the structure so laboriously reared by Pearson and his co-workers over a long span of years. Are new and more pertinent observational data brought into the arena by Dr. Sanders? The answer is no. He has collected no new observations. Has he discovered a new and more potent method of analysis? Again the answer is no.

All that he has done is (1) to criticise the logic of biometric technique (in the first chapter) on grounds and in a manner that we fancy Prof. Pearson could make very fine hash indeed of, if he felt it desirable to take the trouble to do so. (2) To review at length the biological literature (in Chapter 2) that supports the somewhat trite platitude that heredity and environment are inseparable relative to living organisms, each playing a rôle in the determination of every characteristic of every organism. Incidentally we suspect that there lives no biometrician so dumb as not to be aware of this. As might be expected the author finds the idea that acquired characters may be transmitted to the progeny a seductive one. (3) To review at great length an enormous body of literature (in the next five chapters) on the general subject of differential growth in relation to environment. A final chapter sums up the author's conclusions. An indexed bibliography of 65 pages close-set in 8-point type, and a subject index complete the volume.

The book has two merits. The first is the author's insistence, reiterated again and again throughout the book, on the importance of more and more penetrating investigations of the *specific* effects of precisely defined environmental variables upon the human organism, rather than general studies of "heredity *versus* environment." By any technique now conceived of, these latter studies will never *convince* anyone except their protagonists, the boys who did them, on one side or the

other. Dr. Sanders' second significant contribution is his bibliography, and the annotations on it, which is, in effect, what the text of his Part II is. This bibliography will make the book a valuable reference book for a long time to come.

The book is very well produced, and the publisher deserves all praise for undertaking so tremendously expensive an enterprise in times like these.

THE CHANCES OF MORBID INHERITANCE. *Edited by C. P. Blacker. William Wood and Co., Baltimore.* $5.00. 8½ x 5½; xi + 449 + 3 plates + 3 folding charts; 1934.

This symposium on various disease forms which directly or indirectly are supposed or known to be inherited is written especially for the physician faced by the problem of advising his patients on whether they should have children. The diseases discussed are: nervous disorders and epilepsy (W. Russell Brain), mental disorders (A. J. Lewis), mental deficiency (H. Herd), disorders of the eye (Stewart Duke-Elder) and of the ear (E. J. McCann), asthma and other allergic diseases (G. W. Bray), blood (L. J. Witts), cardio-vascular (M. Campbell), renal (A. A. Osman), skin (L. Forman), gastro-intestinal (M. E. Shaw), cretinism and goitre (H. Gardner-Hill), diabetes mellitus and glycosuria (R. D. Lawrence), tuberculosis (E. R. Boland), neoplastic diseases (A. Piney), congenital abnormality of the skeleton (H. A. Harris). Included are also a very good chapter on genetic principles by R. Ruggles Gates and one on the analysis of pedigrees by L. Hogben.

Although not all the subjects have been well treated, some omitting the results of the more recent studies, still it must be said that this represents a very useful contribution. Outstanding and praiseworthy is the fact that the evidence is presented objectively without drawing unwarranted conclusions or attempting to inject eugenics propaganda.

There is a glossary of genetic and psychiatric terms and an index of nine pages. The references are at the end of each chapter.

L'ÉVOLUTION. ADAPTATIONS ET MUTATIONS. *Berceaux et Migrations. Actualités Scientifiques et Industrielles 47. La Paléontologie et les Grands Problèmes de la Biologie Générale.*

By Charles Fraipont and Suzanne Leclerq. Hermann et Cie, Paris. 10 x 6½; 38; 1932 (paper).

ADAPTATIONS ET MUTATIONS. *Position du Problème. Actualités Scientifiques et Industrielles 48. La Paléontologie et les Grands Problèmes de la Biologie Générale.*

By C. Fraipont. Hermann et Cie, Paris. 6 francs. 10 x 6½; 26; 1932 (paper).

These are the first two of a series of five brief monographs by Prof. C. Fraipont and associates in which they discuss different aspects of organic evolution and review the evidence which favors a more or less modified Lamarckism as against the mutation theory.

In the first, the authors summarize Rosa's Ologenesis theory and accept the latter's assertion that each species appears for the first time simultaneously in all parts of the globe where conditions permit its existence. It is only after the species has passed its maturity and is dying that it is gradually restricted to a smaller area. The authors present maps to show the extent of the habitat of different species as it appears from the earlier geologic record and its reduction in later periods or at present. There is no necessity, conclude the authors, to seek a place of origin for the species nor to set up imagined reasons for mass migrations, etc.

In the second, the Lamarckian principle of gradual adaptation is reaffirmed and the author heatedly denies the value of the negative laboratory experiments as proof against the theory.

Is this a true revival of Lamarckism at the hands of paleontologists who have always been partial to it or is it the last flicker of life from old French "die-hards?"

RACING CAPACITY IN THE THOROUGHBRED HORSE. *Part I—The Measure of Racing Capacity. Part II—The Inheritance of Racing Capacity. Carnegie Institution of Washington, Supplementary Publications No. 7.*

By Harry H. Laughlin. Carnegie Institution of Washington, D. C. 50 cents. $9\frac{7}{8}$ x $6\frac{7}{8}$; 26; 1934 (paper).

Two empirical formulas are discussed; one for determining an index of racing capacity of an individual horse in terms of age, sex, weights carried, distances run, and speeds attained; the other, for determining an index of the most probable racing capacity of an individual horse in terms of the racing capacities of its direct and collateral near-kin. In the derivation of both formulas, as has always been the case in attempts to develop single indexes designed to represent complex functional abilities, it was necessary to assign arbitrary weights for the proportional influence of different variables. Whether or not all of the important variables were considered, and whether or not approximately correct weightings were given, obviously, can be known only after the indexes have been used very extensively. It may be presumed, however, that the really important variables were included and that a reasonably satisfactory weighting or stressing of each has been obtained. Unfortunately the observational data on which the study was based are not included and only the most superficial information is given of the analytical methods used.

EMBRYOLOGY AND GENETICS.

By Thomas H. Morgan. Columbia University Press, New York. $3.00. $8\frac{1}{2}$ x $5\frac{1}{2}$; vii + 258; 1934.

Professor Morgan has resorted to several kinds of simplification in order to make his survey of experimental embryology and developmental genetics into a stimulating textbook for college and medical school students and for others in search of an up-to-date and authoritative introduction to these subjects. His aim has been to illustrate the principles underlying development rather than to describe the embryology of individual types in detail, and to make the reader attentive to the logical implications of the data of observation and experiment. Verbal explanations have been replaced whenever possible by illustrations, and bibliographic references have been omitted from the text. There is a selected bibliography in the back of the book, however, and an index.

GENERAL BIOLOGY

STUDIES OF THE WATERS ON THE CONTINENTAL SHELF, CAPE COD TO CHESAPEAKE BAY. *I. The Cycle of Temperature. Papers in Physical Oceanography and Meteorology, published by the Massachusetts Institute of Technology and Woods Hole Oceanographic Institution, Vol. II, No. 4. Contribution No. 34 from the Woods Hole Oceanographic Institution.*

By Henry B. Bigelow. Woods Hole Oceanographic Institution, Woods Hole, Mass. $1.00. 11 x $8\frac{1}{2}$; 135; 1933 (paper).

This paper is a continuation of studies on the thermal status of the waters over the off-shore part of the continental shelf, begun in 1913 by the U. S. Bureau of Fisheries and Museum of Comparative Zoölogy. Cruises for the collection of temperature readings were made during several months of the year from 1927 to 1932. Results are given in tables and graphically in the form of thermal contour lines on outline maps. The author may be commended for a clear-cut and concise report of basic data of first order importance.

THE TEACHING OF BIOLOGY.

By William E. Cole. D. Appleton-Century Co., New York. $2.00. $7\frac{3}{8}$ x 5; xiv + 252; 1934.

This book deals with the teaching of biology as a unified subject, that being the accepted organization for the secondary school. The treatment is from the immediate viewpoint of the teacher, in simple and interesting language, and the treatment is thoroughly modern in the light of educational theory and practice. Features of practical importance are: The abundance of suggested teaching aids;

equipment, use and arrangement of laboratories; and appendices including a classified bibliography, a list of outstanding magazines of science, addresses of scientific supply houses, and forms for survey blanks for a number of local problems in biology. There is a brief but adequate index. The treatment of the subject as a whole will be especially helpful to anyone interested in the teaching of elementary biology.

PRINCIPLES OF ANIMAL BIOLOGY. *Fourth Edition.*

By A. Franklin Shull, with the collaboration of George R. Larue and Alexander G. Ruthven. McGraw-Hill Book Co., New York. $3.50. 9 x 5⅞; xiv + 400; 1934.

LABORATORY DIRECTIONS IN PRINCIPLES OF ANIMAL BIOLOGY. *Fourth Edition.*

By A. Franklin Shull, with the collaboration of George R. Larue and Alexander G. Ruthven. McGraw-Hill Book Co., New York. $1.00. 9 x 5⅞; ix + 100; 1934.

In the present revision of his well-known college textbook the author has directed his efforts towards a greater simplicity in exposition; but, on the whole there is very little difference between this and the previous editions (cf. this REVIEW, Vol. 5, p. 248).

The same can be said for the Fourth edition of *Laboratory Directions* which serves nicely to teach beginners some practical applications of the fundamental principles of biology.

HUMAN BIOLOGY

FRANKLIN PAINE MALL. *The Story of a Mind.*

By Florence R. Sabin. The Johns Hopkins Press, Baltimore. $2.75. 8¼ x 5½; xiii + 342 + 8 plates; 1934.

Franklin P. Mall was unquestionably one of the leading figures in the scientific world of his time. While always zealously and overtly holding faithful to his first love, medicine, he was more than a medical man. For one thing he was one of the acknowledged leaders of his time in biology, and unquestionably had more to do than any other one person with changing the status of human anatomy in this country from being the lowly hand maiden of surgery to a branch of general biology. Again he was no less a leader in altering the outlook of American universities relative to the dignity, the methods, and the spirit of the teaching of science.

He has waited a decade and a half for a biographer. But as he himself would say if he could; it paid to wait! For Dr. Sabin's is a masterly piece of biographic writing—a worthy, just, and adequate treatment of a great subject. And it is done with a devotion that plainly must have made the labor a delight. But fine as is this devotion to the master from a pupil now herself a master, it is not that which makes this a notable book. It is rather the fact that Dr. Sabin has, with great shrewdness and good judgment, set Mall's life as the central jewel in the coruscating background of the most brilliant period of equal length in the progress of the medical sciences that history has yet recorded—"the period of Claude Bernard, Virchow, Cohnheim, Hoppe-Seyler, Schmiedeberg, Lister, Helmholtz, Pasteur, Koch, Ludwig, and His—the period of the foundation of new medical sciences—bacteriology, cellular pathology, biological chemistry, and later immunology." Mall's career as a student started as this period was beginning. He was an important figure in it. The theme is clear and Dr. Sabin has done full justice to it. The book is, in short, a contribution of first-rate importance to the history of ideas, and not just another biography.

The first chapter on early life and education shows how inadequate was the training the Middle West had to offer a boy of Mall's capacities in the '60's and '70's. In the autumn of 1883 he went to Germany, *et incipit vita nova.* During the next three years, first with His and then with Ludwig, his research laid the foundation of his enduring reputation. These were very happy years. At their end he came to Baltimore as a fellow in pathology under Welch in the newly opened Johns Hopkins Medical School. There, except for short interludes at Clark and Chicago, he spent the remainder of his days.

Space is lacking to follow in detail the

course of events in a busy life. The book itself must be read, and then one will see with the utmost clarity how and why Mall influenced students, teaching, research, scientific societies, journals, institutes and foundations as he did. We can do our readers no greater service than to urge them to read this book. For it is *their* book, written for biologists, by a biologist, about a great biologist.

NEGRO-WHITE ADJUSTMENT. *An Investigation and Analysis of Methods in the Interracial Movement in the United States. The History, Philosophy, Program, and Techniques of Ten National Interracial Agencies, Methods Discovered Through a Study of Cases, Situations, and Projects in Race Relations.*

By Paul E. Baker. Association Press, New York. $3.00. 9¼ x 6; 271; 1934.

This study is based on an investigation of ten national interracial agencies in the United States and was presented as part of the work for the degree of Doctor of Philosophy at Columbia University. The first 47 pages have to do with the methods of investigation and the history, philosophy and program of the interrracial agencies. Section III which forms the bulk of the volume is concerned with *A discovery of methods through a study of the activity of interracial agencies in typical situations*. Summing up the results of his study the author finds that

> After this extensive review of the facts our conclusion must be that present attempts to solve American interracial problems are characterized by the presence of two distinct goals and two distinct methods of reaching those goals. These goals are at one extreme a definitely bi-racial society and at the other extreme a completely assimilated race, while the general methods used are either those of conference and coöperation or those of pressure and violence.
>
> On the basis of present trends it seems probable that the conference technique will be used increasingly, but that the conflict method will grow in favor until it effects such reorganization of society as will give the Negro equal status and so make possible the use of the conference technique on an equality basis. If this occurs, the assimilative process will progressively eliminate race differences and so make unnecessary any further interracial effort. If it does not occur, we can envision between the races only continued conflict which palliative methods of adjustment can mitigate but never solve.

The volume concludes with a bibliography and an index.

A CHILD WENT FORTH. *The Autobiography of Dr. Helen MacKnight Doyle.*

By Helen M. Doyle. Gotham House, New York. $3.00. 8 x 5¾; 364; 1934.

Dr. Helen MacKnight Doyle tells vividly her struggles as a pioneer in the practice of medicine. The first part of the book is a personal record of childhood memories of the spacious '80's in California. Grandmother had a lace cap and knew how to make brown gravy. No salad and salted nuts days were those; in fact not until our author was enrolled as one of three women medical students in Toland Hall in old San Francisco did she hear of a salad.

Women were not wanted in the medical schools of those days and were frankly told so, but Helen MacKnight's Scotch stubbornness carried her through her years of study and internship to a practice of her own. There is much of historical interest concerning San Francisco and the Sierra Nevada country but perhaps the most interesting part of the narrative is the struggle for existence of the pioneer women physicians. The first woman student at Toland Hall was told by one of her professors: "A woman has no business to study medicine. If she does, she ought to have her ovaries removed." To this she replied: "If that is true, the men students ought also to have their testicles removed!" As regards the physiological and psychological limitations of women in medicine Dr. Doyle relates that three weeks before her baby was born she attended a woman in confinement and did the same three weeks after. As Mary Austin says in her foreword: ". . . it is difficult to separate Dr. Nellie's success in a difficult and exacting profession from her success as a woman. And in saying that, one has perhaps stated the final judgment of this whole vexed problem of women in professions."

LA RÉVOLUTION DÉMOGRAPHIQUE. *Études et Essais sur les Problèmes de la Population. By Adolphe Landry. Recueil Sirey, Paris.* 25 francs. 9 x 5⅝; 229; 1934 (paper).

The first and larger part of this book (165 pages) contains two long essays on the demographic revolution and depopulation and decadence respectively. The first is a careful, cautious discussion of the falling birth and death rates and the approach to a stable population, with special reference to the consequences in manifold directions of these phenomena, particularly as they apply to France. Nothing very new is developed in the way of results or ideas, but the author has the merits of conservatism and realism. He handles the facts in a scholarly way, and points out with brutal clarity that there is no simple or miraculous solution that can be applied to check or control a tendency towards depopulation once it is well started in any population, and especially in a highly civilized and intelligent one. The second essay discusses the association between depopulation and decadence, chiefly upon the basis of the history of Greece and Rome (the *monde romain*, not Il Duce's home office). Again a scholarly discussion, saturated with pessimism.

What Landry's argument seems to lack is an adequate appreciation of the fact that human biology has been, as yet, but very imperfectly explored; and of no region is this more true than of reproduction. Like Malthus his reasoning and his viewpoint are those of the historiographer and "social scientist"so-called. His pessimism is essentially a mirror image of Malthus's and is quite as likely to be made silly by the unpredicted and still unpredictable course of human reproduction in the mass under the impact of altered circumstances.

The second part of the book reprints four short essays on various aspects of population problems.

BLINDNESS AND THE BLIND IN THE UNITED STATES.

By Harry Best. The Macmillan Co., New York. $6.50. 9¼ x 6¼; xxii + 714; 1934.

An extensive survey which will be found invaluable by social workers and those interested in public health, by legislators, and by physicians. The chief object of the study was to furnish the social economist with a working treatise on a subject which up to the present has been dealt with in a humanitarian rather than in a scientific manner. The blind are regarded as "certain components of the population of the state who demand classification and attention in its machinery of organization." In the seven sections of the survey no important phase of the subject has been neglected. How wide the scope of the book is can best be indicated by picking at random a few of the topics of discussion: Causes of blindness, possibilities of prevention, the blind by sex, by race, by nativity, marital conditions of blind, extent of education among blind, legal treatment, cost, history of education of blind in United States, public and private institutions for the blind, use of raised print, libraries, homes for adult blind and for children, industrial establishments for blind, pensions, indemnity, private associations and public commissions for blind, etc., etc. An enormous amount of statistical data is given; there is a section on conclusions with respect to work for blind, and in a group of five appendices will be found additional tables and illustrations. The volume is indexed.

JAPANESE IN CALIFORNIA. *Based on a Ten per Cent Survey of Japanese in California and Documentary Evidence from Many Sources. Stanford University Publications, University Series. Education-Psychology, Volume 1, Number 2.*

By Edward K. Strong, Jr. Stanford University Press, Stanford University, Calif. $1.00 (paper); $1.50 (cloth). 10 x 6⅞; 188; 1933.

This report, the second in a series of four dealing with Japanese in California, gives extensive data on birthplace, age, sex, size of family, births and deaths, also information on education, occupation and

religious affiliations. The survey, made by twelve people five of whom were of the Japanese race, covered certain definite geographical districts of about 1000 persons each. City, town and country dwellers were represented. Out of a total population in California of 97,456 Japanese, 9,416 (half of whom were children) were personally interviewed. Concerning the birth rate of the first generation in the United States, records show it to be higher than that of the whites, but not as high as frequently has been claimed. The Japanese married man has had about 3.1 children on the average and the Japanese woman 3.3 children. The birthrate of the second generation cannot be estimated for only a handful are old enough to marry but "it would appear that these young people educated in American schools are most likely to imitate their white acquaintances and limit their families very decidedly."

The statistical data are arranged in 68 tables. Included in the report is a section on the distribution of the Japanese in the United States. There is an index.

MATERNAL MORTALITY IN FIFTEEN STATES. *United States Department of Labor, Children's Bureau Publication* No. 223.

U. S. Government Printing Office, Washington. 20 cents. $9\frac{1}{8}$ x $5\frac{7}{8}$; xiv + 234; 1934 (paper).

This report, following the recent publication by the New York Academy of Medicine Committee on Maternal Mortality in New York City in 1930, 1931 and 1932, gives similar data on maternal mortality in 1927 and 1928 for the states Alabama, Kentucky, Maryland, Michigan, Minnesota, Nebraska, New Hampshire, North Dakota, Oregon, Rhode Island, Virginia, Washington, Wisconsin, California and Oklahoma. In both studies, reported cases of puerperal deaths were investigated by trained field personnel, detailed histories of the circumstances of each death were obtained and the data transmitted to their respective committees for analysis. Both committees arrive at much the same general conclusions. It is pointed out that a very large proportion of maternal deaths are preventable; that there is great need for better training of persons responsible for maternal care; that physicians and their organized medical societies must assume the leadership in the field; that the general public must be given widespread education of the importance of prenatal, natal, and postnatal care, the dangers of abortion, and of their own responsibilities. The Children's Bureau is to be commended for carrying through this extensive and valuable investigation. Special praise should go to Dr. Frances Rothert for her clear-cut analysis and well written report.

THE MYSTERY OF STIGMATA. *From Catherine Emmerich to Theresa Neumann.*

By Jeanne Danemarie. Translated from the French by Warre B. Wells. Burns Oates and Washbourne, London. 5 shillings. $7\frac{1}{4}$ x $4\frac{3}{4}$; viii + 248; 1934.

A devout and cultured Roman Catholic with a penchant to describe her own mystic feelings writes this book on stigmata in which she sketches the lives of the nineteenth century stigmatized nun, Anne Catherine Emmerich, her official biographer, Clement Brentano, and her spiritual descendant, Theresa Neumann of Konnersreuth whom the author personally visited. It is on her own personal emotions that Mme. Danemarie dwells so that we learn no more about Theresa Neumann than that which has appeared in numerous articles and books (cf. *Konnersreuth*, noticed in Vol. 8, p. 175 of this REVIEW).

Written in a style *sui generis*, this book and the gentle author also might well have been contemporaries of Jacopone da Todi of whom we are reminded by the following words taken from the introduction: "Here is the story of the journey that led me to the Stigmatised Woman of Bavaria, all athrob with the martyrdom of her wounds and the clairvoyance of her ecstasies."

The work of the translator appears to have been well done.

EARLY DAYS AMONG THE CHEYENNE AND ARAPAHOE INDIANS.

By John H. Seger. Edited by Stanley Vestal. University of Oklahoma Press, Norman. $2.00. 9 x 6; 155; 1934.

This interesting book gives an account of the author's experiences among the Indians in the early years of their life on reservations. Most of the officials of the agency were Quakers, full of the noblest intentions but with little insight into the ways of thought of their Indian charges. They tried to teach the Indians to farm but, quite understandably, the latter preferred the excitement of hunting buffaloes to the drudgery of farming. Seger started as builder and Jack-of-all-trades on the reservation but soon acquired so much prestige among the Indians by his courage and conjuring feats that he was made head of the school for the Indian children. His struggles to maintain discipline among his pupils and their parents, who not infrequently drew a gun or a knife on him, the loyalty of the Indians after he had succeeded in making them his friends, the disputes between the Indians and the white settlers, are all interesting chapters in the history of the relations between the two races. An appendix gives the tribal tradition of the Cheyenne Indians as told to Mr. Seger by one of the chiefs to whom it had been handed down by word of mouth.

THE PEOPLING OF AUSTRALIA. (*Further Studies.*)

By K. H. Bailey, J. B. Brigden, H. Burton, D. B. Copeland, F. W. Eggleston, A. S. Kenyon, F. R. E. Mauldon, H. A. Mullett, G. Packer, P. D. Phillips, W. I. Potter, G. Taylor, S. M. Wadham, A. G. Whitlam. Editorial Committee: F. W. Eggleston, P. D. Phillips, G. Packer, E. Scott, S. S. Addison. Melbourne University Press, Melbourne. 6s. 6d. net. $7\frac{1}{4}$ x $4\frac{3}{4}$; 327; 1933.

In this volume we find a continuation of the investigations on the demographic and intercorrelated economic conditions of Australia (cf. Vol. 5, p. 473 of this REVIEW). The present survey gives a summary of the immigration policy both historically and from the standpoint of the state of public opinion towards new immigration; the limitations imposed by the economic conditions of Australia to an increase in population; the apparent immediate effects of state aided settlements. The several authors limit themselves to an exposition of the facts which can be used to support either of the two opposing viewpoints: limited immigration or lowering of the barriers. Each is consistent *per se* depending on the future; i.e., whether Australia will continue to be an exporting nation or must rely entirely on its own market. In regard to the State planning of communities, all agree that the experience so far has been disastrous for the public exchequer.

CHILD MARRIAGE: *The Indian Minotaur. An Object-Lesson from the Past to the Future. By Eleanor F. Rathbone. George Allen and Unwin, London.* 2s. 5d. net. $7\frac{1}{4}$ x $4\frac{7}{8}$; 138; 1934.

Since 1846 Indian administrators have passed laws tending to curb child marriage so prevalent amongst the natives. These laws have been ineffectual as is known and the author in rather violent manner lays the blame on the English and Indian authorities whom she accuses of fearing the effects of applying such obviously unpopular regulations. The descriptions of the sad state of the Indian woman arouse pity. Early marriage, aside from the grave social burden which it imposes, has as direct evil there the high mortality due to lack of hygienic measures in puerperium. But the author, evidently gifted with a highly developed reform complex, shows lack of political insight in her attack on the already troubled officials, and the short-sightedness common to reformers in her proposed amendments to the latest statutes (Sarda Act). They are three, two of which would permit prosecution by the courts on privately obtained information. In addition, her main method of attack would be to grant greater political franchise to women and arouse then their organized protest. It has apparently not occurred to the author that the fundamental and immediate need is

that of alleviating the hygienic conditions, and that social evolution would follow as a consequence.

KEITH LUCAS.

Contributors: H. H. Turner, F. C. Temple, Sir Walter Fletcher, G. Ll. Hodgkin, E. D. Adrian, Mervyn O'Gorman, Bertram Hopkinson, R. H. Mayo. W. Heffer and Sons, Cambridge. 5 shillings net. 7¼ x 5½; 131; 1934.

After the death of Keith Lucas in the World War Sir Walter Fletcher, with whom he had been associated at Cambridge, intended to prepare a memoir of him and, with this end in view, asked several of Lucas' friends to write accounts of those aspects of his life with which Fletcher was not himself familiar. However, other duties interfered and the memoir was never written. The papers are therefore here published in their original form with the addition of an account by Professor Adrian, a pupil and later a colleague of Lucas, of his life at Cambridge and of his pioneer work on the excitation of nerve and muscle which Adrian himself has continued so brilliantly. The chief impressions which the book leaves are of Lucas' personality, the clearness of thinking which enabled him to state his problems in a form which would permit of an answer, and the mechanical skill with which he constructed his experimental apparatus. A list of his scientific writings is given.

SCIENCE, RELIGION AND MAN.

By William J. J. Cornelius. Williams and Norgate, London. 15 shillings net. 8½ x 5½; 387; 1934.

The author's formal definition of God is "the idea of power exercised by a Spiritual Agency." While for the modern man who does not believe in the existence of God "an absorbing intellectual interest" may be his god "no one can get rid of the necessity of a god." The real nature of God will be revealed. "The adventure we make justifies our action if simply and honestly made, and if proof does not come to us in this life it is because that is reserved for the time when, purified and fit for the vision by transformation, man shall see God as He is." Religion is not so simple and is finally decided to be "incapable of exact definition."

Included in the volume are chapters on magic and a very much condensed survey of various religions, ancient and modern. There is a bibliography and an index.

INCOME IN THE VARIOUS STATES. *Its Sources and Distribution. 1919, 1920, and 1921.*

By Maurice Leven. Based upon Estimates of the National Totals by Willford I. King. National Bureau of Economic Research, New York. $3.50. 9 x 6; 306; 1925.

This book gives estimates for the various states in 1919, 1920, and 1921 of current income—including "(1) wages, salaries and pensions, (2) profits withdrawn from business, (3) dividends, interest, and rent received by individuals, (4) the rental value of homes occupied by their owners, (5) interest upon the sums invested in household furnishings, clothing, and the like, and (6) the value of commodities which families produce for their own consumption"—and gains or losses in the value of property owned. The per capita current income of the Southern states is much below that of the rest of the country when the entire population of each state is considered but the current income of the farm population per farmer and family shows no such wide disparity. There is an index.

OUR PRIMITIVE CONTEMPORARIES.

By George P. Murdock. The Macmillan Co., New York. $5.00; Student edition, $3.60. 7¾ x 5½; xxii + 614; 1934.

This seems to us to be about the best *general* elementary treatise on what the science of ethnology is about, and what its methods and outlook are, that we have yet seen. It digests and condenses an immense amount of original material

published in monographs and books mostly not easily available, and often very dull reading if available, to the end of making plain for some eighteen examples how the "savage" actually lives. It is well written and illustrated. Each of the chapters has at the end a brief but well selected bibliography. There is an excellent detailed index. Altogether we recommend this book without reservation to all students of human biology. Unfortunately many of the half tone illustrations are very badly reproduced.

CLASSIFICATION AND USES OF FINGER PRINTS. (*Seventh Edition*).

By Sir E. R. Henry. His Majesty's Stationery Office, London; The British Library of Information, New York. 3 shillings net (Great Britain); 92 cents (New York). 8½ x 5½; iv + 142; 1934.

All you need to know about finger printing is contained in this the seventh edition of Henry's book. There is an interesting although brief resumé of the history of finger printing and an account of some of the uses which have been made of finger prints. Directions for making prints are given, but the most of the book is devoted to description of the identifying characteristics and classification for filing. This latest revision of Henry's original system (which in turn is based on Galton's) makes it the most widely used system of classification.

THE DOCTOR AND CITIZENSHIP.

By Thurman D. Kitchin. Christopher Publishing House, Boston. $1.50. 8 x 5¼; 89; 1934.

A collection of short essays about the position of medicine in the community, by the President of Wake Forest College. Nothing new or startling is said, and very much that is trite, and for some time since unoriginal. We gather from the book that the author is a sound, genial, and conservative college president.

ZOÖLOGY

IS IT CRUEL? *A Study of the Condition of Captive and Performing Animals.*

By T. H. Gillespie. Herbert Jenkins, London. 6 shillings net. 8½ x 5½; 182 + 16 plates; 1934.

This is a book which will interest all animal lovers and bring solace to those who have deplored the captivity of wild animals. The author, director of the Zoölogical Park in Edinburgh, shows quite conclusively the advantages which a wild animal in captivity has over those that are unconfined, provided of course that the zoo is well kept. In the native state there is constant warfare carried on for the preservation of life. In the zoo, animals very soon adapt themselves to their cages which become to them a safe refuge and frequently develop a real affection for their keepers. A number of instances are cited of animals that, finding means of exit from their enclosures, were accustomed to roam the park at night but always returned before day-break to spend the day in confinement. The rhythmic pacing or movements of the body which so many animals exhibit in captivity Mr. Gillespie believes to be common among many wild animals whether captive or free and enjoyed by them in possibly the same way that the dance is enjoyed by human beings. The second section of the book is devoted to performing animals and the third and final section to the development of zoölogical parks. The volume contains a number of well-chosen illustrations and is indexed.

ANATOMY OF ANIMAL TYPES *for Students of Zoölogy.*

By E. A. Briggs. Angus and Robertson, Sydney. 10s. 6d. 8½ x 5⅜; xix + 250; 1934.

This guide for the study of animal types, both invertebrate and vertebrate, will probably have little practical appeal for American zoölogists since it concerns itself only with Australian forms. The book will undoubtedly find friends in Australia, however, for it seems quite complete, authoritative and clearly

written. The author has purposely omitted using any drawings and diagrams holding the view, ". . . . that practical zoölogy is the study, not of drawings and diagrams, but of animal life in all its phases of structure and function." Whether it is desirable to omit illustrations in this case must be determined by the users of the volume. This conservative reviewer however, used to seeing a picture of an *Amoeba* as he studied it, felt keenly the absence of drawings.

COCCIDIA AND COCCIDIOSIS *of Domesticated, Game and Laboratory Animals and of Man. By Elery R. Becker. Collegiate Press, Ames, Iowa.* $2.50. $9\frac{1}{8}$ x $6\frac{1}{8}$; ix + 147; 1934.

Besides being based on the author's extensive experimental investigations in the field, this book also embodies a digest of the related literature which runs to some 350 references. The work covers information on species, hosts, host-specificity, life cycle, pathogenicity, immunity, prophylaxis and therapeutics. There are twenty-five plates and text figures which are indispensable for identification and description. Three appendices contain: Recommended readings for coccidiosis in hosts not extensively treated in the text, a host-catalogue of genera of coccidia represented in the vertebrates, and notes on technique. There are both author and subject indices.

TROPICAL FISHES *for a Private Aquarium. By Christopher W. Coates. Liveright Publishing Corp., New York.* $2.00. 7 x 5; xi + 226; 1933.

If you have ever had a gold fish you will like this book, although gold fish are not discussed. The foreword says that not all the fishes suitable for aquaria are listed, but there are over a hundred different species in the index, so that one ought to find a fish to meet almost any specifications. There are 57 excellent photographs. The first four chapters are concerned with general information about aquaria, care and feeding of fish, but the bulk of the book is devoted to descriptions of species suitable for pets. This is an excellent book since it not only contains valuable information but is delightful reading as well.

THE ELASMOBRANCH FISHES. *Third Edition. By J. Frank Daniel. University of California Press, Berkeley.* $5.00. $10\frac{1}{4}$ x $6\frac{3}{4}$; xi + 332; 1934.

A third edition of this valuable zoölogical text revised by the addition of new material on the transformation of the endostyle into the thyroid gland; a more complete discussion of the lymphatic system; a consideration of the homologies of the carotid artery between Elasmobranchs and higher Vertebrates, and a report of new studies on the nature of the cells forming the wall of an ampulla of Lorenzini.

KURZE ANWEISUNG FÜR ZOOLOGISCH-SYSTEMATISCHE STUDIEN. *By Bernhard Rensch. Akademische Verlagsgesellschaft, Leipzig.* 6.20 marks. $9\frac{1}{4}$ x $6\frac{1}{4}$; 116 (paper).

This is a most useful and clear discussion of the principles governing taxonomy and terminology. It is designed to explain briefly modern systematic categories and nomenclature to those who are specialists in other fields of biology, but need nevertheless some understanding of systematic zoology. There is a final section of sound advice to the prospective *Systematiker*. The book is not overladen with examples and consequently makes easy as well as highly instructive reading.

INSECTS AS MATERIAL FOR STUDY. *Two Inaugural Lectures Delivered on 17 and 24 November 1933. By G. D. Hale Carpenter. Oxford University Press, New York.* $1.00. 9 x 6; 38; 1934 (paper).

Two short essays, delivered as lectures, present the author's opinions as to the desirability of insect material for the study

of biological problems. In general, Professor Carpenter is impressed with the insects as subjects to be used in analyzing problems of ecology and evolution. Of especial interest are the author's views as to the adaptive value of mimicry and protective coloration among insects and the relation of these phenomena to natural selection.

THE TERRARIUM. *Tortoises, Other Reptiles and Amphibians in Captivity.*

By Burgess Barnett. Poultry World, London. 1s. 6d. net. $7\frac{1}{4}$ x $4\frac{7}{8}$; 57; no date (paper).

A book designed to popularize the "quiet delights of reptiles and amphibians as pets." It includes directions as to feeding and housing and descriptions of such species of reptiles and amphibians as are suitable for vivaria and greenhouses.

BOTANY

THE COMPARATIVE ANATOMY OF EXTRA-CHROMOSOMAL TYPES IN DATURA STRAMONIUM. *Carnegie Institution of Washington Publication No. 451*

By Edmund W. Sinnott, Helen Houghtaling and Albert F. Blakeslee. Carnegie Institution, Washington, D. C. $1.50 (paper); $2.50 (cloth). 10 x $6\frac{3}{4}$; 50 + 19 plates; 1934.

This quantitative analysis of the histological characters of *Datura* mutants of known chromosomal constitution is principally concerned with the structure of the floral pedicel; the leaves of the various types were relatively constant in structure, the stem never really stops developing and comparable sections are hard to find, and the roots were too highly variable within one and the same type for comparison with other types. As might have been expected, the various polyploid types, 1n, 2n, 3n, and 4n showed differences in cell and organ size corresponding to their chromosome content. The principal point of interest is the analysis of heteroploid types, diploid plants with a single extra chromosome. Primary mutants differ very little from the structure of diploid plants but secondary mutants tend to have vascular bundles which are distinctly wider and greater in area than those of diploid. The differences between mutants were mostly of a quantitative character. Besides tables of data there are photomicrographs of representative flower stalks of each of the mutants. As the first histological study of plant hybrids that is not limited to the F_1 generation this contribution deserves the attention of geneticists.

THE FLORA OF ICELAND AND THE FÆROES. *By C. H. Ostenfeld and Johs. Gröntved. Levin and Munksgaard, Copenhagen.* D. Cr. 6.50. $7\frac{7}{8}$ x $5\frac{1}{8}$; xxiv + 195 + 2 maps; 1934.

The senior author finished the first half only of this descriptive manual before his death in 1931 and the work was completed by Johs. Gröntved of Copenhagen with the assistance of specialists on several of the difficult genera like *Hieracium* and *Salix*. It provides analytical keys for the identification of the vascular cryptogams and the seed plants of Iceland and the Færoes, with notes on their distribution and on the colloquial names by which they are known to the inhabitants. There are maps to make the place names intelligible, and there are glossaries and indices which make the book readily usable. It is interesting to note that about half of the genera are represented by only one species. This flora should be very useful to students of plant distribution since many North American plants are represented.

THE MYXOMYCETES. *A Descriptive List of the Known Species with Special Reference to Those Occurring in North America.*

By Thomas H. Macbride and G. W. Martin. The Macmillan Co., New York. $6.00. $9\frac{1}{4}$ x $6\frac{1}{4}$; x + 339 + 21 plates; 1934.

This manual is a monographic treatment of the myxomycetes of the world based

on the senior author's *The North American Slime Moulds* and amplified to include all the species thus far described. Analytical keys and full descriptions are provided with critical notes on each species. The taxonomy of these forms presents considerable difficulty and since discriminations between names and authorities necessarily must be made frequently it is a commendable thing to discuss the reasons for the choice as fully as the authors have. Considerable space is given to lists of synonyms and citations of the original descriptions. There is an index and a bibliography. There are 21 plates illustrating habit, spore form, and structure of a large number of species.

DAYLILIES. *The Wild Species and Garden Clones, Both Old and New, of the Genus Hemerocallis.*

By A. B. Stout. The Macmillan Co., New York. $3.00. $9\frac{1}{4}$ x $6\frac{1}{4}$; x + 119 + 36 plates; 1934.

The collections of daylilies at the New York Botanical Garden provided the material on which this manual is based. It describes the species and horticultural clones grown in this country in some detail and there are recommendations as to soils, treatment, and suitability for the garden. There are numerous photographs, four color plates reprinted from Addisonia, a key to species, and an index. Altogether it should be a very satisfactory book for horticulturists and gardeners.

EPITOME OF BOTANY WITH QUESTIONS AND ANSWERS. *Part 1.*

By G. A. Kapadia. G. A. Kapadia, Rothfield St., Broach, India. 8 annas. $7\frac{1}{4}$ x $4\frac{7}{8}$; 44; 1933 (paper).

This syllabus has about the same content and style as a well-bred student's notes on a lecture course on plant morphology. The principal object is to teach the student the names of the structures which have diagnostic value in classification. There is a short, unillustrated glossary of botanical terms, a list of Greek and Latin root-words, and a list of questions on the material covered in the booklet. Although this could be used to supplement a second-rate textbook profitably there would be no advantage in using it with a good textbook.

A TEXTBOOK OF SYSTEMATIC BOTANY. *Second Edition.*

By Deane B. Swingle. McGraw-Hill Book Co., New York. $2.25. 9 x $5\frac{7}{8}$; xv + 270; 1934.

This is the second edition of a college textbook planned not only to teach students how to identify plants and to provide them with glossaries and diagrams to aid in interpreting the standard manuals, but also to introduce them to the logical principles underlying schemes of classification. Brief synopses are given of 60 families of spermatophytes. There is an index and there are lists of reference books.

MORPHOLOGY

INTERCORTICAL SYSTEMS OF THE HUMAN CEREBRUM. *Mapped by Means of New Anatomic Methods.*

By Joshua Rosett. Columbia University Press, New York. $3.00. 10 x 7; xvi + 135; 1933.

In this book the author describes his work in mapping out the intercortical nerve fibres by the ingenious method, devised by him, of dissecting the tissues along the natural lines of cleavage by exploding them with gas. Although much more work will have to be done before definite results can be obtained concerning special regions and functional mechanisms, the work is important as orientation for further study. Adolf Meyer contributes a foreword and Stanley Cobb a preface. The bibliography contains 65 titles and there is an index.

L'Utilisation de la Charpente Osseuse par les Animaux Vertébrés. *Deuxième édition revue et augmentée.*

By Louis Perbal. G. Doin et Cie, Paris. 25 francs. 9½ x 6¼; 162; 1934 (paper).

The author has added about 60 pages to his earlier edition noticed in Volume 7, p. 476 of the Review, but leaves us still unconvinced that his examples of adaptation of skeletal structures of animals prove conclusively that the Lamarckian theories of evolution are so.

PHYSIOLOGY AND PATHOLOGY

Features in the Architecture of Physiological Function.

By Joseph Barcroft. The University Press, Cambridge; The Macmillan Co., New York. $5.50. 8½ x 5½; x + 368; 1934.

The argument that runs through this series of lectures is that the fundamental principles of human physiology are interdependent, that in a certain sense one principle implies the others.

> At the outset I had regarded the body as a noble building on the principles which it exhibits as unconnected features in its architecture. It became clear that the features were far from being independent. The highest functions of the nervous system demand a quite special constancy in the composition of its intimate environment. The stability of the internal *milieu* almost compels the principle of the storage of materials and of integration in adaptation. Again an easy stepping stone to integration in [is] the practice of the body to have more than one way of doing many things. But parallel mechanisms may express themselves not only in integrative but in antagonistic processes. Moreover, increased function actively may be achieved either by heightening the efforts of units already functioning or marshalling a greater number of units; and so we arrive at the "all-or-none" relation.
>
> It seemed almost as though there had emerged an approach to physiology from an unusual angle: not from that of mere structure, whether the structure of organs or of chemical formulae, but from the principles of function.

This, then, is the outline of a thoroughgoing and critical review of quantitative evidence on which this series of propositions rests presented skillfully in the form of lectures. It is an impressive chain of reasoning but it would be unfair to say that it makes easy reading; it requires careful study but it is worth it. Bibliographies and an index are provided.

Studies on the Possible Intoxicating Action of 3.2 per Cent Beer.

By A. J. Carlson, N. Kleitman, C. W. Muehlberger, F. C. McLean, H. Gullicksen and R. B. Carlson. University of Chicago Press, Chicago. 75 cents. 9 x 5⅞; vii + 85; 1934 (paper).

A laboratory experiment designed to be helpful in a redefinition of alcoholic intoxication in its social and legal aspects. The specific question to be answered was: Can sufficient beer containing 3.2 per cent alcohol be consumed to produce definite intoxication? The beer was given to human subjects under experimental conditions. The measurements taken were: Alcoholic concentration in blood and urine, a series of objective performance tests, and subjective judgments of change in behavior of the subjects by observers. The amounts of beer given were graded from two 12-ounce bottles up to quantities taxing the capacity of the digestive tract with repetition of dosage at various time intervals and with and without food. A check test was carried out using near beer. The data are presented in tables, charts and correlation surfaces. A brief review of experiments dealing with intoxication is made, but an extensive comparison of the findings is impossible for lack of statistical data in previous studies. The authors found that forced consumption of 3.2 per cent beer at the rate of 4 to 6 bottles per hour for three and one-half hours (109 cc.–190 cc. of alcohol) produced intoxication in five out of 29 cases. The average blood concentration of alcohol was 1.2 milligrams per cc., which was within the range where 40–46 per cent were found "under the influence" or at the stage of "stimulation" by other investigators, and this concentration is below the limit of intoxication set by the British Alcohol Investigation Committee. The authors conclude that 3.2 per cent beer is not intoxicating, for the ordinary person cannot practically drink large enough quantities

necessary to reach the required alcohol concentration in the blood.

DISEASES PECULIAR TO CIVILIZED MAN. *Clinical Management and Surgical Treatment.* *By George Crile. Edited by Amy Rowland. The Macmillan Co., New York.* $5.00. 8½ x 5½; xi + 427 + folding chart; 1934.

The principle enunciated here is that the high activity of the brain, the thyroid, and the adrenal-sympathetic system of civilized man gives him not only his unique power and distinction, but also his unique diseases, neurocirculatory asthenia, hyperthyroidism, peptic ulcer and probably diabetes. Treatment of these hyperkinetic syndromes includes one or more points of attack, the object in each case being to lessen the factors that are causing the damaging kinetic drive; thus the driving power of the brain may be lessened by rationalization or by excision of the sympathetic ganglia, the driving power of the thyroid decreased by thyroidectomy or by interference with its sympathetic nerve supply by ligation, the hyperactivity of the adrenals by denervation. Of these possible points of attack, primary emphasis is placed on adrenal denervation. Under this treatment, 94 per cent of 76 cases of true neurocirculatory asthenia, the same percentage of 79 cases of hyperthyroidism, and 96 per cent of 37 cases of peptic ulcer, showed cure or improvement.

Approximately the first one-third of the book deals with the development of the theory of the interrelated hyperkinetic activity of the brain-thyroid-adrenal-sympathetic system, clinical descriptions of the "diseases peculiar to civilized man" and the surgical technique of adrenal denervation. The remainder of the book is devoted to routine clinical histories of patients, most of whom were treated by adrenal denervation. Although joint authorship is not noted on the title page, parts of the book are contributed either by or with the assistance of five coworkers. In its entirety, however, the book reveals the boundless enthusiasm and unbridled optimism of the principal author. An extensive bibliography and name and subject indexes are included.

LES ULTRAVIRUS. *Pathogènes et Saprophytes. Techniques d'Étude. Caractères Physiques et Biologiques. Maladies à Ultravirus. Clinique. Anatomo-Pathologie. Épidémiologie. Immunité.* *By Paul Hauduroy. Masson et Cie, Paris.* 60 francs. 10 x 6½; 462; 1934 (paper).

Although this might be called a second edition of the author's book *Les Ultravirus et les Formes Filtrantes des Microbes* published in 1929 and noticed in these columns (Vol. 5, pp. 364–365) it is really a different work. Interest and research on the viruses has advanced to such an extent as to add to, modify or negate much of the material presented in the previous work. The arrangement of the section dealing with specific viruses—those affecting bacteria, plants, fishes, insects, and birds as well as mammals—follows in the main that of the earlier work, but it has been entirely rewritten to conform with the knowledge which subsequent research has brought to light. The author has added a section on techniques as bases for further study, but has omitted the discussion of filtrable forms of non-filtrable germs, as he intends to devote another book to this phase. The book is well-written, well documented and indexed, and should altogether make a worthy addition to the bacteriologist's library.

L'IMMUNITÉ PAR MÉCANISME PHYSICO-CHIMIQUE. *By R. Dujarric de la Rivière. Masson et Cie, Paris.* 18 francs. 9½ x 6½; 73; 1934 (paper).

For ten years the author has conducted numerous investigations to determine the physicochemical mechanism underlying immunity. In this volume he briefly summarizes the results of a few of his experiments as an illustration of the value of biochemical and biophysical methods and technique. The monograph is divided into three parts. In the first he reports the changes occurring in the antiseptic power of certain compounds through the action of ultraviolet radiation and in relation to difference in electrolytic disassociation. The second treats of the preciseness of the flocculation technique from which

Ramon's work on diphtheria anti-toxin derives its importance. In the last and most extensive part the author demonstrates the function of the hemoglobin, adsorption and transportation of toxins and antitoxins, and in particular the effect of bismuth, arsenic and mercury compounds on the red blood cells of man (syphilitic and non-syphilitic) and other animals.

DIET AND PERSONALITY. *Fitting Food to Type and Environment.*

By L. Jean Bogert. The Macmillan Co., New York. $2.00. $7\frac{3}{4}$ x $5\frac{1}{4}$; ix + 223; 1934.

Advice as to what to eat and when to eat it is not lacking in the lives of most of us. Sensible advice, that which is free from superstitious prejudice or is not advanced for the commercial advantage of somebody and which takes any account whatsoever of individual differences is not however, accessible to a vast number of persons. In this book Doctor Bogert presents, in clear although somewhat breezy style, most of what the relatively new science of nutrition has to teach the practical man about his diet. In addition, as she says in the Foreword, "You may find that I have almost as much to say about general living conditions and health habits as about diet, but that is because no one can profit from a good diet as much as he should, when his habits of living are wrong . . . ."

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome VII. Sang et Lymphe. Réactions d'Immunité. (Deuxième Édition).*

By Ch. Achard, Justin-Besançon, A. Besredka, Léon Binet, J. Bordet, L. Cuénot, H. Delaunay, R. Fabre, J. Jolly, M. Laudat, Ph. Pagniez, G.-H. Roger, E. Schulmann, P.-E. Weil, E. Zunz. Published under the direction of G.-H. Roger and Léon Binet. Masson et Cie, Paris. 100 francs (paper); 120 francs (cloth). $9\frac{5}{8}$ x $6\frac{5}{8}$; xii + 731; 1934.

Since 1927 when the first edition of this volume (noticed in these columns, Vol. 3, p. 143) of a useful reference work on physiology appeared research has increased the knowledge concerning blood and lymph to such an extent that the material had to be thoroughly revised and augmented to make the second edition up-to-date. Notable additions include a chapter on the chemical constituents of blood written by M. Laudat, and one by L. Cuénot on the coagulation of the blood in the invertebrates. A chapter by Edgard Zunz on coagulation has been substituted for Doyon's treatment of the subject which appeared in the first edition. The documentation has likewise been brought up through 1933 and the whole book is more than 200 pages longer than the earlier work.

HOMMAGE À LA MÉMOIRE DU PROFESSEUR JEAN CANTACUZÈNE. *Tome I et II.*

Masson et Cie, Paris. 250 francs. 11 x $7\frac{1}{2}$; xv + 822; 1934 (paper).

Doctor Ion Cantacuzino was born in Rumania, completed his medical and bacteriological education in Paris, was connected for several years with the Pasteur Institute, and for the last thirty-two years of his life occupied the Chair of Experimental Medicine in the Faculty of Medicine and the Institute of Pathology and Bacteriology in Bucharest. He died in January of this year. It was originally planned to present these two volumes of papers by his students and friends to him on the occasion of his seventieth birthday in November.

The papers treat of bacteriological and pathological subjects. The list of contributors is a long and imposing one, but space permits us to mention only a few: A. Besredka, A. Boquet, A. Calmette, S. Metalnikov, L. Nègre, P. Reiss, G. Teissier and A. Wadsworth.

A short biography of Doctor Cantacuzino and a list of his publications, 123 in number, are provided.

LOCALIZATION OF FUNCTION IN THE CEREBRAL CORTEX. *An Investigation of the Most Recent Advances. Proceedings of the Associa-*

tion, New York, December 28th and 29th, 1932.

By Association for Research in Nervous and Mental Disease. Editorial Board: Samuel T. Orton, John F. Fulton and Thomas K. Davis. The Williams & Wilkins Co., Baltimore. $8.00. 9 x 5⅞; xxi + 667; 1934.

A series of papers by thirty-four well known contributors, on aspects of cerebral localization, presented at the thirteenth annual meeting of the Association for Research in Nervous and Mental Diseases on December 28–29, 1932. The volume is divided into three sections representing three different attacks on the problem. The first, the anatomical, indicates the structural differences of various parts of the cortex; the second section deals with the experimental aspect which points towards the variation in functional importance of the same cortical area in animals of different phylogenetic levels. The third attack is from the standpoint of detailed clinical observation, particularly on people who have undergone lobectomies.

THE HUMAN BODY. *Its Structure and Activities and the Conditions of Its Healthy Working.*

By H. Newell Martin. Twelfth Edition, Thoroughly Revised by Ernest G. Martin. Henry Holt and Co., New York. $4.00. 8½ x 5½; xv + 701; 1934.

The twelfth edition of this excellent textbook follows the pattern of the preceding one but is augmented and modified in accordance with recent discoveries. It is as complete and clear an outline of human anatomy and physiology as could possibly be written for the college student.

BIOCHEMISTRY

THE PHYSICO-CHEMICAL PROPERTIES OF PLANT SAPS IN RELATION TO PHYTOGEOGRAPHY. *Data on Native Vegetation in its Natural Environment.*

By J. Arthur Harris. Compiled from Original Records and Edited by a Committee of Dr. Harris' Colleagues in the University of Minnesota. University of Minnesota Press, Minneapolis. $4.50. 9¼ x 6; vi + 339; 1934.

A unique situation is involved in the publication of this volume. The laboratory records and field notes of the late J. Arthur Harris collected over a period of about eighteen years and hitherto unpublished have been collected and tabulated by men formerly associated with him, and are now offered to physiologically-minded ecologists for interpretation. Professor Harris undertook a very extensive survey of the physico-chemical properties of the tissue fluids of representative plants from very diverse ecological habitats intending to "analyze the data from two standpoints: first, the extent to which the plant's adaptability to environment—as measured by its ability to vary the physico-chemical properties of its tissue fluids—is a factor in plant geography and the evolutionary process; and, second, the physical and chemical properties of the environment as a determining factor in the distribution of plant forms." His data include depression of the freezing point of the expressed sap and the osmotic pressure calculated therefrom; the specific electrical conductivity, expressed in ohms; pH value, chloride content and sulphate content; and for each plant the full scientific name and notes on its habitat. About 12,000 such records are presented here in systematic fashion and the problem of indexing and cross-indexing and coding has been very nicely solved. There is no attempt at analysis or interpretation. There are, however, notes by Harris setting forth his objectives and explaining his methods, and there is a bibliography of the 44 papers he and his collaborators published on this subject.

It seems to us that this undertaking is an interesting experiment in scholarship; at the death of a competent investigator a large amount of data, too important to be lost, falls into the hands of his literary executors. How can it best be used? This is one way of solving the problem; we are curious to see how it works out.

A Biochemical Study of the Metabolism of Mental Work. *Archives of Psychology No. 164.*

By Hyman Goldstein. Archives of Psychology, Columbia University, New York. $1.00. 9½ x 6¼; 57; 1934 (paper).

An important contribution to studies in physiological psychology. The work is divided into two sections: (1) Investigations of tasks involving mental work with overt physical components (cancellation, intelligence test and tapping). The conclusions drawn were that

> Increase of the physical component results in greater metabolic change as determined by the biochemical methods employed in this investigation,
>
> Increase of the mental component without increase of physical component does not result in greater metabolic change, as determined by the biochemical methods used in this study.

(2) Investigation of tasks involving mental work with minimum physical component. These studies showed that

> Metabolic change, as determined by the biochemical methods of this investigation, does not differ significantly from that which occurs during "no work."

In a discussion of the results obtained the author expresses the belief that

> If there are any effects produced by mental work *per se* upon the total metabolic activity, it is evident that the current biochemical methods, particularly those employed in this study, do not appear to be sufficiently sensitive to detect these effects.

There may still be very intense biochemical activity present in particular areas of the brain as a result of mental work without affecting the total body metabolism. The author presents the results of his experiments in tabular form and concludes with a literature list of 67 titles.

Handbuch der Biologischen Arbeitsmethoden. *Lieferung 428. Quantitative Stoffwechseluntersuchungen.* Containing following articles: *Technik der Messung des Gesamtstoffwechsels und des Energiebedarfes von Haustieren*, by Francis G. Benedict, V. Coropatchinsky and Ernest G. Ritzman; *Zwei elektrisch kompensierte Emissions-Kalorimeter für kleine Tiere und Säuglinge und für Erwachsene*, by Francis G. Benedict.

Urban und Schwarzenberg, Berlin. 6.50 marks. 10 x 7; pp. 619–750; 1934 (paper).

The first of the papers describes the buildings, stalls, and apparatus developed at the Agricultural Experiment Station at Durham, New Hampshire, for respiration and nutrition studies on cattle and horses. No one who has ever lived on a farm can fail to be impressed by the automatic mechanical device, described and illustrated in detail, for the collection, removal, and storage of manure.

The second paper describes two types of a differential calorimeter much better adapted for short time metabolism experiments on man and small animals than the older and more massive chambers which sometimes weighed fifteen times as much as the person being studied.

Both papers are thorough and are well illustrated.

The Chemistry of the Hormones.

By Benjamin Harrow and Carl P. Sherwin. Williams & Wilkins Co., Baltimore. $2.50. 9 x 6; vii + 227; 1934.

A practical book for the laboratory worker who wishes to prepare active hormone fractions of a chemically pure hormone. The main emphasis is on the chemical procedure. However, of necessity, considerable biological information is woven into the very clearly written exposition. Historical information with reference to discoveries and development of techniques forms a secondary but interesting phase of the discourse. There is a chapter devoted to each of the following: Thyroid; parathyroid; pituitary; adrenal; male, female and plant hormones; insulin; and secretion. Each chapter has its extensive list of references, and the volume is indexed by author and by subject.

Medizinische Kolloidlehre. *Lieferungen 10 und 11.*

Edited by L. Lichtwitz, Raph. Ed. Liesegang and Karl Spiro. Theodor Steinkopff, Dresden. 5 marks each. 10⅜ x 7⅜; Lief. 10, pp. 689–768; Lief. 11, pp. 769–848; 1934 (paper).

Previous numbers of this series on the

application of colloid research to medicine have been noticed at various times in these columns. The present *Lieferungen* contain the following papers: Liver and gall; spleen, both by K. Hinsberg and T. Wedekind; The lung and upper respiratory tract and the nervous system, by R. E. Liesegang; The smallest organisms and disinfection, by H. Reiche; Dietetics of childhood with special consideration of milk, by K. Scheer; Dietetics of adults, by W. Heupke, and H. Lampert; and Balneology, by R. E. Liesegang.

ANNUAL REVIEW OF BIOCHEMISTRY. *Volume III.*

Edited by James M. Luck. Stanford University Press, Stanford University, Calif. $5.00. $8\frac{3}{4}$ x 6; viii + 558; 1934.

The third annual volume of this exceedingly useful review of selected topics in biochemistry is as well done as its predecessors. There is a good deal of flexibility in the choice of the subject matter treated; some topics are reviewed only biennially, and some less active fields are to be treated more infrequently still. Two subjects appear for the first time in this volume, reviews of the biochemistry of malignant tissues and of dentistry.

INTRODUCTION TO PHYSIOLOGICAL CHEMISTRY. *Third Edition.*

By Meyer Bodansky. John Wiley and Sons, New York. $4.00 net. 9 x $5\frac{7}{8}$; xi + 662; 1934.

Many sections of the third edition of this excellent textbook have been revised to include new data which have appeared since the last edition. The discussions of the chemistry of enzymes, the regulation of gastric activity, muscle metabolism, the mineral requirements in nutrition, the vitamines, hormones, blood and other body fluids, have been enlarged.

ÉLÉMENTS DE CHIMIE ORGANIQUE BIOLOGIQUE. *Introduction Chimique à l'Étude de la Biologie Générale.*

By Michel Polonovski and Albert Lespagnol. Masson et Cie, Paris. 100 francs. 10 x $6\frac{1}{2}$; 594; 1934 (paper).

This is an excellent, systematically arranged introduction to biochemistry. All the groups of compounds basic to plant and animal life are discussed, and technical instructions given. Although primarily intended for the use of physiologists, the biologist, physician, pharmacologist and chemist should find it a handy reference book. The index is very complete.

SEX

THE REVOLUTIONARY IDEAS OF THE MARQUIS DE SADE.

By Geoffrey Gorer. Wishart and Co., London. 8s. 6d. net. $8\frac{5}{8}$ x $5\frac{1}{2}$; 264; 1934.

The portrait which Mr. Gorer draws of the Marquis de Sade is very different from the fabulous monster of tradition. De Sade was a radical in politics and an experimentalist in sex. In the former capacity he made influential enemies who used his sexual experiments as a pretext to ruin him.

> . . . if de Sade on several occasions indulged in abnormal pleasures, he also risked his life to save that of a woman who had caused him to be imprisoned for thirteen years; . . . if a psychologist has attached his name to a form of cruelty, he was actually an inveterate opponent of capital punishment.

In his political writings de Sade escaped the uncritical optimism which led many of his contemporaries to look forward to an immediate establishment of Utopia.

> He had no illusions about the natural goodness of man, but he believed that with complete economic and sexual equality human conditions could be greatly bettered. He anticipated the views of Malthus on population, and the tolerance of the Danish penal code as regards sexual behaviour.

As a writer on the psychology of sex de Sade was a pioneer in a significant field of human biology. Unfortunately, however important the study of the sexual perversions may be, its spectacular character has had the effect of drawing away the atten-

tion of investigators of sexual psychology from the still more important study of normal sexual behavior. Mr. Gorer considers that Krafft-Ebing's definition of sadism as "sexual emotion associated with the wish to inflict pain and use violence" reflects a misunderstanding of de Sade's own viewpoint and that it would be preferable to use Schrenck-Notzing's term algolagnia for all activities in which sex and external pain are united and to "keep the word Sadism for the special group of instincts which de Sade was the first and almost the only person to describe and which constitutes by far his most important contribution to psychology." Mr. Gorer's proposed redefinition of sadism is "the pleasure felt from the observed modifications on the external world produced by the observer. . . . Like all human emotions this is ambivalent, and can be either constructive or destructive." In other words Mr. Gorer would equate sadism with the pleasure of self-expression.

> . . . there can be Sadistic satisfaction in painting a picture, but not in painting a house under another person's orders and following another person's taste; there can be Sadistic pleasure in killing a person, but not if that killing is ordered and independent of the killer.

The book includes a foreword by J. B. S. Haldane and a bibliography covering four pages of books by and about de Sade, but unfortunately it lacks an index.

GENEALOGY OF SEX. *Sex in its Myriad Forms, from the One-Celled Animal to the Human Being.*

By Curt Thesing. Translated from the German by Eden and Cedar Paul. Emerson Books, New York. $5.00. 8½ x 5½; xii + 286; 1934.

This book on sex is interesting. Some biologists may consider it sensational and anthropomorphic, and some specialists (as specialists alone can do) will undoubtedly find factual errors within; nevertheless, the writings capture the interest of the reader and hold it. The author has collected a commendable number of natural history observations dealing with various behavior reactions associated with sexual processes throughout much of the animal world. He has arranged the material in the form of a 'genealogy' in that he attempts to depict the development of the sex impulse and its consummation from primitive to complex forms. He discusses the sex secrets of spiders, squid, crayfish and toads with the same realistic enthusiasm as he shows in dealing with the human organism. The book merits reading. [Reginald the Office Boy liked the last chapter best.]

RECENT ADVANCES IN SEX AND REPRODUCTIVE PHYSIOLOGY.

By J. M. Robson. P. Blakiston's Son and Co., Philadelphia. $4.00 net. 7⅞ x 5⅛; x + 249; 1934.

This book really is what the title says it is—recent work on sex physiology. A knowledge of the anatomy and physiology of sex organs is assumed and the chief topic considered is the recent work on the sex hormones. There is no single list of references, but separate lists are given at the end of each chapter. The citations are much abbreviated, titles of the papers not being included. There is, however, an author index and a good subject index.

BIOMETRY

CONTINUOUS INVESTIGATION INTO THE MORTALITY OF ASSURED LIVES. *Statistics for the Six Years 1924–1929.*

Published on behalf of The Institute of Actuaries and The Faculty of Actuaries in Scotland. University Press, Cambridge; The Macmillan Co., New York. $15.00. 9¾ x 6; xxxiv + 675; 1933.

This book tabulates the combined experience of a large number of British and a few Canadian and Australian life insurance companies for the years 1924–1926 and 1927–1929. Policy holders subject to extra risk are excluded. Medically examined lives and those not medically examined are treated independently, while under each section the four classes of insurance—whole life with profits, whole life without profits, endowment with profits,

and endowment without profits—are tabulated separately. In each table the deaths and policies in force as well as the exposed to risk and unsmoothed rate of mortality based on them are given. The total experience represents over ten million person-years of exposure to risk and 121,094 deaths.

BIOMETRIA E ANTROPOMETRIA. *Trattato Elementare di Statistica Vol. III.*

By Marcello Boldrini. Antonino Giuffrè, Milano. L. 50. $9\frac{1}{2}$ x $6\frac{1}{2}$; xiii + 464; 1934.

This is one of a series of volumes on elementary statistics published under the auspices of the Istituto Centrale di Statistica of Italy. It summarizes rather thoroughly, although often with ineffectual criticism, statistical applications in the field of biology: problems of growth, evolution, genetics, anthropology, somatic constitution. The exposition is very clear and the bibliography complete. There is an index of eighteen pages.

PSYCHOLOGY AND BEHAVIOR

MODES OF BEHAVIORAL ADAPTATION IN CHIMPANZEE TO MULTIPLE-CHOICE PROBLEMS. *Comparative Psychology Monographs, Vol. 10, No. 1, Serial No. 47.*

By Robert M. Yerkes. The Johns Hopkins Press, Baltimore. $1.50. 10 x $6\frac{7}{8}$; 108; 1934 (paper).

Unfortunately the results of this interesting series of experiments can only briefly be given. Four sexually immature chimpanzees (3 female, 1 male) served as subjects in the experiments which were undertaken to determine "(*a*) whether, and if so under what conditions, solution of a certain type of novel problem occurs suddenly, as if by discovery and with insight; (*b*) optimal motivational conditions for problem solution; (*c*) whether adaptation to relational problems may be achieved in radically different ways, as by trial and error versus discovery." Of 24 problems 14 (58%) resulted in solution. In 6 of the 14 cases the error was abruptly eliminated after 3 or more mistakes. The remaining 8 successful adaptations were mostly achieved by "gradual approximation to perfection of response." The experiments are given in detail together with their summary in tabular and graphic form. The author believes that the following practically and theoretically significant generalizations are justified:

(*a*) Motivational factors are of two sorts, barring intermediates and mixtures; (1) those which primarily influence general activity, interest, and alertness, and (2) those which affect specific responses. In this investigation the former appeared to be indispensable, whereas the latter were of slight or even negative value.

(*b*) Given excellent general adaptation to the experimental situation and the experimenter, together with willingness to coöperate by making the circuit through the multiple-choice apparatus a certain number of times daily, marked stimulation by the use of motivational factors interfered with the solution of relational problems by chimpanzee.

(*c*) It is indicated that special rewards and deterrents neither reënforced correct responses nor inhibited incorrect responses, for the fairly obvious reason that the same response might be correct for one setting of the apparatus and incorrect for the next."

The study concludes with a brief list of references.

A FIELD STUDY OF THE BEHAVIOR AND SOCIAL RELATIONS OF HOWLING MONKEYS. *Comparative Psychology Monographs, Vol. 10, No. 2, Serial No. 48.*

By C. R. Carpenter. The Johns Hopkins Press, Baltimore. $2.25. 10 x $6\frac{7}{8}$; 168; 1934 (paper).

The author spent about eight months studying howling monkeys in the Panama Canal Zone and in the Republic of Panama. Most of the intensive study was made on the Island of Barro Colorado, where it was possible to keep groups under observation day after day.

The howling monkeys live in clans varying in size from four to 35 individuals. A clan tends to occupy a definite and limited territory through which it moves in reference to lodge and food trees at about the rate of eight hundred yards per day. The males usually lead the group and when they encounter potential danger, or other groups of howlers, noisy vocal battles result and the group soon shifts its course

to avoid contact. The author sometimes met with howls and bluff, often accompanied with showers of sticks and dung, before flight or indifference was shown.

Among adults in a group the sex ratio is approximately 28 per cent males to 72 per cent females. Mating is apparently communal with some preference among individuals. The males are peaceful and coöperative toward all members of the clan. At times single males become separated from a clan and frequently when these complemental males attempt to join a strange group they are driven away temporarily by vigorous vocalization.

The young are infants in arms for about one month, then they ride their mother's hip until nearly a year old. During the second year the young follow the mother more or less closely. The young are weaned and the tendency for play is at its height. Toward the end of the third year play habits decline, sexual development takes place and the young become sober old monkeys.

There are sixteen pages of illustrative plates, a bibliography of 74 titles, and an index to this very interesting study of monkey society.

THE PHILOSOPHY AND PSYCHOLOGY OF SENSATION.

By Charles Hartshorne. University of Chicago Press, Chicago. $3.00. 9 x 6; xiv + 288; 1934.

Here we have presented to us the theory of the Affective Continuum which, according to the author, is the foundation of intersensory resemblances. It implies that whatever qualities exist can be related as variables intersecting in the same system. It also implies that qualities of human experience correspond in some degrees to the qualities of neural and somatic cellular experiences which by the bond of sympathy which is the psycho-physical relation, form their physiological conditions." A characteristic example will render the meaning clearer: "the smell of a skunk—which in moderate intensity may be enjoyed—is a bitter like smell, a bitterness differently spatialized from that of the taste of strychnine, but plainly akin to it."

The greater part of this work deals especially with visual and auditory sensations. Aside from minor inaccuracies such as that the wave-length of the visible spectrum is from 400 to 800 millimeters, we are introduced to a derivation of the affective continuum, e.g., "the brightness of highly pitched sounds." The author affirms that if this fact and its implications had been seriously considered by physiologists, the Wever-Bray phenomenon would have been discovered long ago. Not being a philosopher we cannot understand how nor where the author derives the erroneous assertions that nobody is deaf to the brightness range (the upper limit of which is apparently regarded by the author as 800 cycles).

From the viewpoint of an empiricist, the examples given above, together with the statement that some of the evidence discussed is based only on intuition, the disregard of experimental data and last but not least the appendix on the applicability of the affective continuum to theology, are sufficient to classify this book as an attempt to reduce psychology to its primitive sterile status. In our opinion the author achieves clearness of language and expression only in discussing matter of his own specialty and we find worthy of particular praise his pages on aesthetics.

WHO SHALL SURVIVE? *A New Approach to the Problem of Human Interrelations.*

By J. L. Moreno. Nervous and Mental Disease Publishing Co., Washington. $4.00. 9⅛ x 6; xvi + 440; 1934.

The student of human relations will find this an interesting book. The author first experienced the need for some definite method of social and psychological planning when a member of a staff which was supervising a group of 10,000 Austrians of Italian extraction who were moved during the World War from their homes in the southern Tyrol to a place near Vienna. The throwing together of such a large group, unselected, unaccustomed to the environment, and unadjusted within themselves produced great unhappiness and friction. To bring about a better social adjustment within this group Dr. Moreno began his first experiments in sociometric planning, later carrying on and extending

and refining his methods among groups in this country, chiefly in public and training schools in and near New York City. He has also been concerned with the psychological planning of communities for the Department of the Interior. Briefly, socionomy is a science which is concerned with the psychological properties of populations and with the communal problems which these properties produce. Sociometry is the mathematical study of these psychological properties. The amount of organization shown by social groups is measured by the sociometric test. By means of this test an individual can make his choice, without restraint, for membership in the group for which he is best fitted. In one of the last sections in the volume the writer discusses the importance of maintaining the *spontaneability* of the individual which requires the concentration of all agencies—technological, psychological and eugenic. The experimental work is illustrated by numerous charts and graphs. Further notes, a glossary, and a bibliography are included in a series of supplements. The volume is indexed.

THE BEHAVIOUR OF ANIMALS. *An Introduction to its Study.*

By E. S. Russell. Longmans, Green and Co., New York. $4.20. $8\frac{1}{2}$ x $5\frac{3}{8}$; viii + 184; 1934.

A book which cannot fail to interest its readers. It should be in all biological as well as general libraries. For the general reader interested in natural history no better introduction to the study of animal behavior has appeared. Likewise all students intending to specialize in this line of work will find it valuable reading. Stress is placed on the importance of regarding the animal as an entity rather than studying it as a mere bundle of mechanisms responding to stimuli, on observing and recording fully and accurately an animal's behavior in its daily activities, not only what is unusual but even the simplest responses. The author believes that much valuable knowledge of animal behavior is possessed by game keepers, shepherds, dog breeders, etc. which the professional student has generally ignored. He does not find Roule's theory that the salmon, when ready to spawn seeks increased quantities of dissolved oxygen in fresh water streams, sufficient to explain why this species seeks a particular estuary or a particular stream which at its mouth frequently contains heavily polluted water which it must pass through before reaching the fresher water. The volume is adequately illustrated, each chapter is well documented and there is an index.

YOU MUST RELAX. *A Practical Method of Reducing the Strain of Modern Living.*

By Edmund Jacobson. Whittlesey House, McGraw-Hill Book Co., New York. $1.50. $7\frac{1}{2}$ x 5; xv + 201; 1934.

A "handy" book (third printing), based on the author's earlier work *Progressive Relaxation*, whereby Americans can keep up their fast pace of living without too great a strain on the system. Dr. Jacobson, of the University of Chicago, has for many years devoted his attention to neuromuscular tensions and the disabilities which they produce. He has developed a method of relaxation which he strongly recommends to all those who, while physically fit, suffer from exhaustion, insomnia, or nervousness of one kind or another. He gives detailed instructions on *how* to relax properly even while being active. Progressive relaxation under his system frequently brings improvement where there is no organic disease in cases of indigestion and colitis and he believes that some advancement is being made by the same method in the little understood field of hypertension. Written expressly for the layman the volume is devoid of technicalities. It contains a number of illustrations but is without index.

MECHANISMS OF HANDEDNESS IN THE RAT. *Comparative Psychology Monographs, Vol. 9, No. 6, Serial No. 46.*

By Geo. M. Peterson. The Johns Hopkins Press, Baltimore. $1.25. 10 x $6\frac{7}{8}$; 67; 1934 (paper).

Right and left handedness seem to occur in

about equal numbers with rats, the ambidexterity occurring less frequently than either of the other conditions. Handedness seems to be a stable characteristic though relatively complex. Chance use or previous experience cannot entirely account for the trait for ambidextrous animals do not acquire a fixed preference for one hand after a greater amount of forced practice with that hand. Seven generations of inbreeding were insufficient to establish a simple Mendelian mechanism for the inheritance of the trait. Cerebral localization of handedness lies in the frontal area of the contralateral hemisphere. Destruction amounting to less than 4 per cent of the area of one hemisphere will lead to transfer in the preferential use of the hands.

Twenty pages of appendices give the tabulated test data, and two pages of plates give 28 diagrams of local cerebral destruction relative to certain rats under test. There is a bibliography of 23 titles.

INTRODUCTION TO PHYSIOLOGICAL PSYCHOLOGY.

By Graydon LaV. Freeman. Ronald Press Co., New York. $4.50. 8 x 5⅜; xvii + 579; 1934.

One is tempted to characterize this book as psychology in terms of axial gradients. But that is hardly fair as it would seem to imply that the author is riding a hobby which is not the case. There is more of what is generally taught as biology than is usual in a psychology text. This is to be expected from the author's definition: "the field of physiological psychology covers these investigations and interests which lie between psychology, physiology, and neurology, and which are not paramount to any one of them. It is, in a sense, a hybrid, like physiological chemistry, and serves to emphasize the essential continuity of the sciences."

The book is divided into four main divisions: Basic neural mechanisms in behavior, Structuro-functional organization of neural mechanisms, and Integrative action of neural mechanisms, and neural mechanisms and variable behavior. There are selected references at the ends of the chapters as well as the regular literature citations given in foot-notes. The index includes both authors and subjects.

KEEPING A SOUND MIND.

By John J. B. Morgan. The Macmillan Co., New York. $2.00. 7¾ x 5¼; ix + 440; 1934.

This book puts the findings of psychologists and psychiatrists on mental hygiene into non-technical language for the benefit primarily of college students. Its viewpoint is that mental health depends in large part on the formation of certain mental habits and the elimination of certain others. The chief factor which leads in extreme cases to the functional mental diseases and in less extreme cases to unhappiness and inefficiency is the refusal in one form or other to face reality. Particularly dangerous is the habit of blaming others for our failures. The ascetic ideology which assumes that to be meritorious an activity must be distasteful is also the cause of much maladjustment. "Modern researches have demonstrated that work is man's best friend. It is a means of prophylaxis against mental disease and a therapeutic agent for effecting cures." The book contains a two-page list of references for further reading and an index.

INTRODUCTION TO COMPARATIVE PSYCHOLOGY.

By Carl J. Warden, Thomas N. Jenkins and Lucien H. Warner. Ronald Press Co., New York. $4.50. 8 x 5⅜; x + 581; 1934.

This is an excellent reference or text-book, bringing together widely scattered material on the behavior of infra-human organisms. The present volume is an abridged and simplified edition of a larger and more detailed work by the same authors to be called *Comparative Psychology*.

The first six chapters are somewhat general, giving historical background, general aspects of behavior and methods of testing capacities. The last 14 chapters are devoted to the description of the reactions of the different phyla. The same topical

arrangement is maintained from group to group; so one can follow, protective behavior, for example, from amoeba to monkeys. Although that particular subject fares pretty poorly, the book is a storehouse of information.

There are subject and author indices.

CIVILIZED LIFE. *The Principles and Applications of Social Psychology. A Revision and Enlargement of Social Psychology, 1925.*

By Knight Dunlap. The Williams & Wilkins Co., Baltimore. $4.00. $8\frac{1}{2}$ x $5\frac{1}{2}$; ix + 374; 1934.

This is a revised and enlarged edition of the author's *Social Psychology*, which was noticed in Volume 1, page 137 of this REVIEW. Chapters have been added on desire, race and civilization, and the child as a member of the group. Professor Dunlap intends to elaborate the topics of the family, religion, and politics in separate treatises which will deal with them in more detail than is possible in the present book. An index and an annotated bibliography, in which he tells—sometimes quite pungently—what he thinks of the books cited, are included.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

CLARET *and the White Wines of Bordeaux.*

By Maurice Healy. Constable and Co., London. 5 shillings net. $7\frac{3}{8}$ x $4\frac{7}{8}$; 165; 1934.

This volume well maintains the high standard set by the earlier volumes of the Constable Wine Series. The *grands vins* of Bordeaux are, at their best, the superlatively best examples of God's major gift to the gustatory and associated senses of mankind.

[Reginald the Office Boy says this is too strong a statement, likely to lead some paranoiac weaned on Burgundy or Rioja to shoot up the office. He is wrong. We have understated the facts. And in any case magnanimity and reasonableness are our strong points. Should any one feel an urge to prove to us by example that there are better wines than the best of Bordeaux, here we are, ready and waiting. No more willing guinea pig ever offered himself for experimentation!]

Mr. Healy knows his clarets and sauternes, and rates them, on the whole, very fairly and justly. He describes the processes of their growth and manufacture in considerable detail, and gives excellent advice about buying, storing, and serving them. Naturally the bulk of the book goes to the red wines. There isn't much that can be said about a Chateau Yquem of a great year except to be as lyrical as your powers permit, once and for all, and then maintain a reverend peace. It is good to talk about wine, yes, but still better to drink it.

There are some odd biological facts and problems about Bordeaux wines that Mr. Healy touches upon. One of them completely floored Pasteur, by his own admission, after a considerable struggle.

ATTENDING MARVELS. *A Patagonian Journal.*

By George G. Simpson. The Macmillan Co., New York. $3.00. $9\frac{1}{4}$ x $6\frac{1}{4}$; xiii + 295 + 15 plates; 1934.

This is an extremely entertaining book. The author, Associate Curator of Vertebrate Paleontology at the American Museum went to Patagonia to collect fossils, where they grow weird ones for reasons that he makes quite plausible even to those not nurtured on geology. The first thing he did was to run head on into a lively sort of revolution, barely escaping serious consequences. Then with a truck and assorted helpers as time went on he ranged over the pampas, certainly one of the most literally God-forsaken countries in which civilized human beings habitually move and have their beings. The essence of Patagonia is *wind*—lots of it. Air in a tremendous hurry to get somewhere else, in short. And worse, this aerial urge is so nearly perennial as to make no matter.

The author writes both vividly and logically. The result is an amazingly good book, that tells the reader what he really wants to know about the physiography, fauna, flora, the people and their manners and customs, the history, confection and virtues of the national drink *yerba maté*, and a thousand other things. The book is well illustrated with photographs, but unfortunately lacks an index.

THE PHILOSOPHICAL WRITINGS OF LEIBNIZ. *Everyman's Library Volume No. 905.*
Selected and Translated by Mary Morris. *E. P. Dutton and Co., New York.* 90 cents. $6\frac{3}{4}$ x $4\frac{1}{4}$; xxxiii + 284; 1934.

This *Everyman's Library* edition of selections from Leibniz's philosophical writings includes the *Monadology; Principles of Nature and of Grace, Founded on Reason;* and *On the Ultimate Origination of Things*. These are given complete. In order to show the development of Leibniz's philosophy extracts are also given from his correspondence with Foucher, Arnauld, Bayle and Clarke, and from his *Exposition and Defence of the New System* and *New Essays on the Human Understanding*. Finally in order "to illustrate the breadth and variety of Leibniz's interests, and also his attitude to other men of learning of his time," a number of miscellaneous extracts from his writings are selected. The book includes an introduction by C. R. Morris, a bibliographical note, an annotated index of proper names, and a philosophical index.

SEVEN FAMOUS NOVELS BY H. G. WELLS. *The Time Machine. The Island of Dr. Moreau. The Invisible Man. The War of the Worlds. The First Men in the Moon. The Food of the Gods. In the Days of the Comet.*
By H. G. Wells. *Alfred A. Knopf, New York.* $2.75. $8\frac{1}{4}$ x $5\frac{1}{2}$; xi + 860; 1934.

H. G. Wells started what may properly be called his career as a biologist. He has never wholly forsaken the outlook and habits of thought indoctrinated in the South Kensington laboratory. Many of his readers feel that the seven novels here reissued are, taken as a lot, the best work he has ever done. They are, in the order of this edition, *The Time Machine; The Island of Dr. Moreau; The Invisible Man; The War of the Worlds; The First Men in the Moon; The Food of the Gods; In the Days of the Comet*. They are, one and all, biological romances *au fond*, and no one without training in biology can get the full savour of them. The publisher has done a real service in making these stories readily available in beautiful format and at an amazingly low price.

SIXTH REPORT OF THE UNITED STATES GEOGRAPHIC BOARD, 1890 *to* 1932.
U. S. Government Printing Office, Washington. 80 cents. $9\frac{1}{8}$ x $5\frac{7}{8}$; ix + 834; 1933 (paper).

This report contains all important decisions made by the Board from 1890 up to June 1932. There is an interesting discussion of the problem of making names, and an equally interesting account of the history of the organization. Pages 76–834 are devoted to an alphabetical list of foreign and national geographical names approved by the Board.

THE COST OF BIOLOGICAL BOOKS IN 1934

By JOHN R. MINER

Department of Biology, School of Hygiene and Public Health, Johns Hopkins University

FOLLOWING the usual custom of the QUARTERLY REVIEW OF BIOLOGY the present paper is devoted to a report on the cost of books which have been reviewed during 1934. In a reference in *Nature* to "The Cost of Biological Books in 1933" the question was raised whether the rubric "England" in Tables 1 and 2 did not include books published in Scotland. This is true; we apologize to all good Scotsmen for this unintentional slight and change the rubric "England" to "Great Britain," and "English-American" to "British-American" with the understanding that in all previous reports these two rubrics include books published in Scotland. The prices of foreign books were converted into dollars on the basis of the exchange at the time the books were received.

TABLE 1

Prices of Biological Books, 1934

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
Germany	7,811	$147.34	1.89
British-American	13,443	195.35	1.45
France	12,041	120.22	1.00
Great Britain	14,152	135.87	0.96
United States	65,959	616.51	0.93
British Government	488	4.35	0.89
Other countries	6,715	57.75	0.86
U. S. Government	3,267	6.00	0.18

The total number of pages reviewed in 1934 is 123,876, an increase of 18.3 per cent over 1933 and of 50.0 per cent over 1926.

Table 2 shows the price trends of books published in various countries from 1926 to 1934 and the absolute and relative changes in price from 1933 to 1934 and from 1926 to 1934. Figure 1, plotted on an arithlog scale, compares the price trends for Germany, France, Great Britain and the United States. The average price per page of foreign biological books in terms of United States currency has in general increased from 1933 to 1934. Only the books published by the British Government have shown a decrease in price and these form too small a sample to be reliable. This increase is no doubt attributable, at least in part, to Mr. Roosevelt's noble experiment with the dollar. On the other hand, the trend of price of biological books published in the United States is still downward. As a result of these opposite trends of foreign and domestic books the average price per page of all the books reviewed in 1934 has changed but little, being 1.036 cents, an increase of 3.1 per cent over 1933 but a decrease of 5.6 per cent from 1926.

The price, in terms of the dollar, of books published in Great Britain has increased nearly one-half from 1933 to 1934, but is still 25 per cent below the 1926 price. French books, which until 1933 were the least expensive of any commercially printed books, have increased in price by more than a third from 1933 to 1934, and are now nearly triple the 1926 price. German books are again the most expensive of all. As was noted in the report for 1933 the high prices of German scientific books and periodicals have worked great hardship to both libraries and individual

TABLE 2

Comparison of the Prices of Biological Books from 1926 to 1934

ORIGIN	AVERAGE PRICE PER PAGE									CHANGE + OR − FROM 1933 TO 1934		CHANGE + OR − FROM 1926 TO 1934	
	1926	1927	1928	1929	1930	1931	1932	1933	1934	Absolute	Relative	Absolute	Relative
	cents	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*per cent*	*cents*	*per cent*
British-American	1.55	1.39	1.46	1.90	1.91	2.27	1.48	1.29	1.45	+0.16	+12.4	−0.10	−6.5
Other countries	1.51	0.78	1.13*	1.68	0.97	1.53	1.02	0.85	0.86	+0.01	+1.2	−0.65	−43.0
Great Britain	1.28	1.14	1.09	1.29	1.13	1.19	0.89	0.66	0.96	+0.30	+45.5	−0.32	−25.0
United States	1.12	1.09	1.14	1.14	1.09	1.05	1.00	1.02	0.93	−0.09	−8.8	−0.19	−17.0
Germany	1.09	1.20	1.48	1.65	1.82	1.75	1.60	1.43	1.89	+0.46	+32.2	+0.80	+73.4
British Government		0.96	1.26	0.39	1.19	1.03	1.45	1.39	0.89	−0.50	−36.0	−0.07†	−7.3†
France	0.35	0.36	0.45	0.47	0.47	0.69	0.60	0.74	1.00	+0.26	+35.1	+0.65	+185.7
U. S. Government	0.31	0.24	0.21	0.23	0.30	0.28	0.36	0.17	0.18	+0.01	+5.9	−0.13	−41.9

* With two special treatises omitted as explained in Vol. 3, p. 601.

† Change from 1927 to 1934.

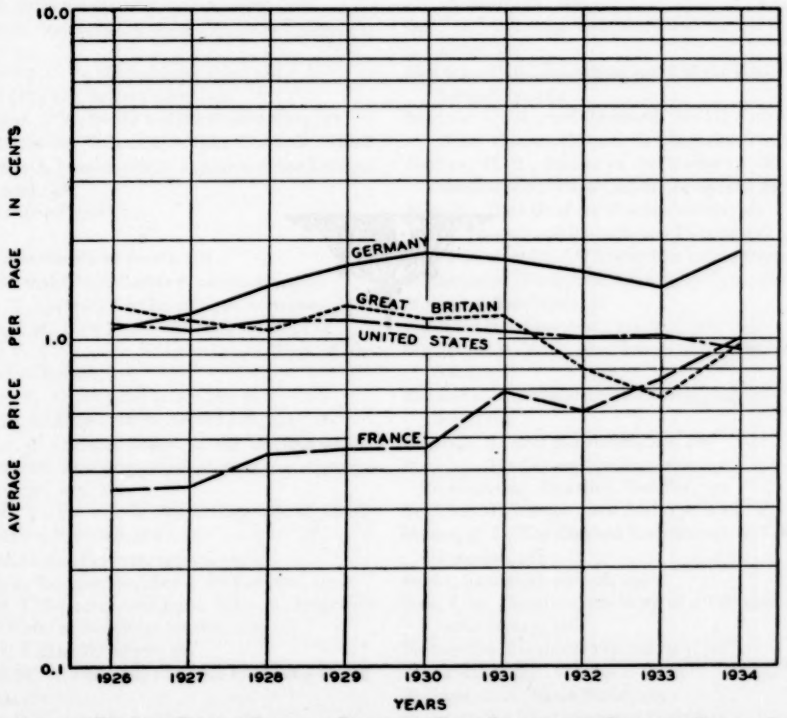

FIG. 1. AVERAGE PRICE PER PAGE IN CENTS FOR BIOLOGICAL BOOKS PUBLISHED IN GERMANY, FRANCE, GREAT BRITAIN AND THE UNITED STATES FROM 1926 TO 1934

scientists; so much so that the Medical Library Association recommended that, unless prices were reduced, libraries should cancel their subscriptions to the most expensive journals. As a result of conferences with the German publishers reductions in the prices of scientific periodicals have been made, but evidently these reductions do not extend to scientific books.

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